The evolutionary ecology of decorating behaviour

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Abstract

Many animals decorate themselves through the accumulation of environmental material on their exterior. Decoration has been studied across a range of different taxa, but there are substantial limits to current understanding. Decoration in non-humans appears to function predominantly in defence against predators and parasites, although an adaptive function is often assumed rather than comprehensively demonstrated. It seems predominantly an aquatic phenomenon – presumably because buoyancy helps reduce energetic costs associated with carrying the decorative material. In terrestrial examples, decorating is relatively common in the larval stages of insects. Insects are small and thus able to generate the power to carry a greater mass of material relative to their own body weight. In adult forms the need to be lightweight for flight likely rules out decoration. We emphasise that both benefits and costs to decoration are rarely quantified, and that costs should include those associated with collecting as well as carrying the material.

Keywords: camouflage, covering, crypsis, masking, ornamenting, shield carrying

Introduction

We review the literature on species that decorate their bodies with material from the environment, to highlight the depth of current understanding, and to determine if we can identify general trends in the distribution and functioning of this trait. The adaptive consequences of animal coloration have become a highly active research area in the last decade, and (since decoration often strikingly alters the decorator's appearance) it is now timely to explore the state of current knowledge regarding non-human decorators. The behaviour that we call *decorating* has variously been called *covering*, *ornamenting*, *masking*, *hatting*, *carrying*, *shield-carrying* and *trash-carrying* [1]. Berke et al. [1] provided the most explicit definition to date:

"*We define a decorator as any animal that actively attaches foreign material to itself or to its biogenic structure. Thus, we exclude the passive accumulation of debris and structure-building itself; for example a polychaete tube of mucous-bound sand is not decorated, whereas a tube which is enhanced with shell and algal fragments is decorated*."

It might be beneficial to refine this definition for several reasons. Although it is important to exclude passive accumulation of debris, decorative accumulation can be achieved through specific behaviour, or morphology, or a combination of the two that aid in the attachment and/or retention of material, and such traits should have been subject to selection for that purpose. The word foreign may also be confusing, since in some cases the material involved is the animal's own waste products; *environmental material* might be a more suitable phrase. We consider waste produced by the animals to be part of this environmental material, but not specialist self-generated materials (like silk in some invertebrates and secreted oils in vertebrates). Lastly, we think there is value in restricting decorating to attachment to the organism itself and not to "its biogenic structure". The polychaete tube mentioned in Berke et al.'s description illustrates our concern that in many cases it would be difficult to distinguish between material that is fundamental to the physical integrity of the structure and that which is "decoration".

One further issue remains, which is differentiating “decoration” from “tool use”. Tool use has been subject to a number of definitions, the most widely used is by Beck [2]:

“the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.”

Since it has been difficult to settle on a universally-applicable definition of tool-use, it should not be surprising that it is difficult to unambiguously separate tool use from decoration. In general, material used for decoration is attached to the organism, whereas tools are generally held or gripped using muscle power. Tools are generally held for shorter periods of time, whereas decoration is a longer-term process. A tool also is a single discrete entity whose orientation is vital to its functioning; whereas decoration generally involves the accumulation of numerous materials whose orientation with respect to each other is not vital to functioning. However, as illustrated later, there are grey areas in this demarcation between decoration and tool use.

Taking these issues into account, we define a decorator as:

an organism that (by means of specialist behaviour and/or morphology that has been favoured by selection for that purpose) accumulates and retains environmental material that becomes attached to the exterior of the decorator.

Decorator crabs

The most widely studied group of decorators are crabs of the superfamily *Majoidea*. The group has over 900 species, about 75% of which show decorating over some or all of their body, having specialised hooked setae to attach material from the environment. The adaptive value of this decorating seems to be anti-predatory. Although such benefits to decorating are often postulated, this is an unusual case where anti-predator benefits have been demonstrated against free-living predators in the natural environment. Several studies [3-5] have found that experimentally altering or removing decoration increased vulnerability to predators. In the laboratory, Thanh et al. [6] found that in the presence of a perceived predatory threat there was a decrease in decorating with increased presence of competitively dominant crabs, with this effect being stronger in juveniles than adults. The authors interpreted this as suggestive that juveniles were more at risk of predation than adults, and that perceived predatory risk induced increased aggression related to competition for decorating materials. In support of this, the extent of decorating material on an individual was a good predictor of dominance in aggressive encounters. Stachowicz and Hay [3] found no effect of perceived predation risk on decorating. These authors argued that decoration required hours of activity (which might heighten exposure to predators), and so one would not expect to see variation in decoration in response to shorter-term fluctuations in perceived predation risk.

The mechanisms underlying anti-predatory effects like those above are not well established. Items used in decoration are often chemically-defended plants or sessile animals, and it seems plausible that predators detect the crab but actively avoid attacking because of repellent smell or taste from the decorations. However, not all decorations provide the animal with chemical defence, and it is likely that decoration often functions through crypsis via background matching, masquerade and/or disruption. Majoids are generally sedentary, and Hultgren & Stachowicz [8] argued that they most often decorate on the rostrum, which conceals the antennae whose movement might make crabs particularly visible. Hultgren & Stachowicz consider and reject other possible functions. Food storage seems unlikely as there is no strong correlation between dietary items and items used in decoration. There is also currently little evidence of use in intraspecific signalling; and a role in hiding them from their prey is unlikely when most crab species prey on animals that cannot mount active defence against an approaching predator.

It would seem useful to further explore the behaviour of such crabs under enhanced predation risk (for instance, olfactory cues of predatory fish) in a laboratory setting. If the primary defensive function is camouflage, then we might expect (for example) movement away from the source of the olfactory cues, reduced movement, hiding in physical structures, or changed substrate choice. Given our understanding of crypsis by background matching and by disruptive camouflage [8], It should also be possible to analyse images of crabs on preferred substrates to determine whether their match to the background is enhanced post-decoration and through what mechanisms.

Crabs show reduced decoration with increasing size; this effect is seen both in within-species and between-species comparisons [9]. Berke & Woodlin [10] have demonstrated that carrying decorations can be energetically expensive (see later), and hypothesized that predation risk reduces with increasing size, potentially because predators such as fish are gape-limited, and/or larger crabs can more effectively defend themselves with their claws and through possession of a thicker carapace (see [4] for similar arguments). Thus the reduction in decorating with increasing size may be driven by differential changes in the costs and benefits of carrying decorations.

Other aquatic organisms

Wicksten [11] documented carrying behaviour in at least four families of brachyuran crabs. This involves shorter 5th and sometimes 4th legs that are no longer used for locomotion but to lift an object (e.g. a shell, piece of sponge or coral, or rock) over the dorsal aspect of the posterior part of the carapace. She speculated that this may act as a physical barrier against predators, as visual or chemical camouflage, or as food storage, but no direct evidence has been offered in support of any of these functions.

Dayton et al. [12] provide another rare demonstration of an anti-predator function under field conditions. In staged encounters, Antarctic sea urchins decorated with hydroids were protected from attack by anemones, but were invariably killed in a repeat encounter after the hydroids had been removed. McClintock & Janssen [13] studied a pelagic Antarctic amphipod that often carries a gastropod. In laboratory experiments they found that amphipods actively captured the gastropod and that carrying behaviour offered protection against predatory fish. Ross [14] demonstrated in the laboratory that octopus failed in attacks on hermit crabs carrying a sea anemone on their shell, with previous work demonstrating that the crabs actively transfer anemones onto themselves. Subsequently, a number of studies have demonstrated that hermit crabs obtain anti-predator protection from sea anemones and hydroids on their shell ([15]), but evidence of active facilitation of such association is often absent.

Numerous species of sea urchins and gastropods of the family Xenophoridae cover themselves with small rocks, shells and algal fragments. Some cover themselves for days or weeks at a time, others for only a few hours. Dumont et al. [16] provided laboratory experiments that found that for two urchin species presence of wave surge and moving algal blades significantly increased propensity to show this behaviour. The authors interpreted this as suggestive that covering reduces mechanical damage caused by abrasion and dislodgement. Blades slide freely over covered urchins but can become entangled in the spines of uncovered ones, leading to dislodgement or spine breakage. Exposure to UV light also increased covering, suggesting a photo-protective selective mechanism. Amsler et al. [17] demonstrated in another urchin species that covering decreased the ability of a predatory sea anemone to kill the urchin. Covering has also been observed in deep-water sea urchins where risks of UV damage, dislodgement, or abrasion seem unimportant in a study by Pawson & Pawson [18]. They speculate that costs of covering may be felt in increased locomotive costs of foraging and in decreased ability to flee quickly from predators. In the field they observed that urchins essentially abandon covering after reaching a certain size; they argue that this critical size matches a switch from sit-and-wait foraging to more extensive-search foraging (where locomotive costs would be more important).

The larvae of many caddisfly (insect order Trichoptera) construct cases out of various environmental materials bound together with silk. These cases are carried around, and even when feeding or moving most of the organism remains inside the case. Cases offer physical protection from predators in staged encounters in the laboratory [19,20], and may also function to reduce danger through being swept from the substrate in lotic environments [21].

Terrestrial species

Larvae of a wide range of insects carry so-called "shields" of material [22]. Faecal material is a prominent feature of these shields. The larvae drop their exuviae after each mould, but in many cases collect them (together with their faeces) on two spines at their abdominal tip. It is widely believed that the primary function of this shield is anti-predatory and/or anti-parasitoid, and there is experimental support for this in the laboratory by Bacher & Luder [23]. They conducted field experiments showing the shield of their focal species offered no effective defence against the main predator (a paper wasp), but was highly effective defence against parasitoid wasps. They found no protection against UV-B in the laboratory. A number of studies also demonstrated a protective function against at least some predators in the laboratory [24]. Sometimes the protection appears physical in nature, preventing predators with short mouthparts from being able to contact the larva [25]. There is also evidence of chemical protection, with shield protection being diminished if it remains physically intact but chemically changed either by solvent-leaching or by manipulation of larval diet [26]. Nakhira & Arakawa [27] demonstrated that the "trash-package" of juvenile lacewing *Mallada desjardinsi* reduced both the likelihood that ladybirds that encountered a lacewing would attack it, and the probability that such an attack was successful; offering both crypsis and a physical defence. Larvae of the green lacewing *Chrysopa slossonae* prey on the wooly alder aphid *Prociphilus tesselatus*. A larva actively transfers waxy wool from the bodies of captured prey and places them on its own body. Eisner et al. [28] demonstrated that this decoration provides defence against the ants that tend the aphids: experimentally denuded larvae where seized and removed by ants, whereas intact larvae where apparently unrecognised and left untouched.

Decorating may also provide visual camouflage to some insect larvae. An example is the "backpack" carried by the assassin bug (*family Reduviidae*) made out of the carcasses of its ant prey. Jackson &

Pollard [29] demonstrated that jumping spiders (Salticidae) more readily attacked lures made from a bug without a backpack than a bug with a backpack, which the authors interpret as the spiders readily identifying naked bugs as prey but not those with backpacks. This result held regardless of the relative size of masked and naked bugs. The authors feel that this was a failure to detect the masked bugs as prey, rather than a failure to detect them as an entity; since they reported that to human observers back-packed bugs were readily detected against the background.

Decorations may also provide distinct defence in different modalities against varied predator groups. For example, Brandt & Mahsberg [30] investigated the nymphs of two assassin bugs (*Paredocla* spp. and *Acanthaspis* spp.), commonly called ant bugs because of their diet. They found that geckos, centipedes and selenopid spiders all had more difficulty capturing ant bugs with backpacks than those without in staged encounters. The spider attacked both treatments of bugs readily, but when the spider grabbed back-packed bugs the backpack came away in the grip of the spider often allowing the bug to flee. Centipedes attacked only naked bugs, which the authors put down to tactile and chemosensory cues of the backpack masking the presence of the bug. The same interpretation was given with respect to the geckos, but involving vision as the primary sensory modality. These assassin bugs often have two layers of decoration: a covering of dust, sand and soil particles (a dust-coat) and the “backpack” of ant prey corpses and plant parts. Whilst the backpack seemed key to anti-predator survival, the dust coat seemed to play a role in preventing recognition by ant prey. Experiments with three different ant species [30] suggested that the dust coat impeded chemical and/or tactile recognition of the assassin bugs but that the backpack had a minor role in this. Other assassin bugs may use decorations for aggressive purposes. The assassin bug *Salyavata variegata* seems to live within termite nests preying on the termites, it actively covers itself in pieces of the carton wall of the nest and this seems to offer chemosensory and tactile background matching, as guard termites routinely pass over the bugs, tapping them repeatedly with antennae and palps without attacking [31].

Camouflage also seems to be a function of decoration in other terrestrial groups. Duncan et al. [32] show that two unrelated desert-dwelling spiders have independently evolved very similar setal morphology that aids in the retention of sand over the body and presumably acts in concealment. The presence of exogenous material (soil, sand, debris, etc.) on the cuticle has been reported across several spider families [33]. This article reported that modified setae of the crab spiders *Stephanopis spp.* fasten debris from the bark that they typically rest on. It further reported that such debris improved brightness background matching but not colour matching, and interprets the setae as an anti-predatory adaptation.

In birds, a range of species add substances to their feathers that alter their appearance (termed cosmetic coloration and reviewed by Delhey et al. [34]). In most cases these are self-secreted preen oils, but in some cases these are environmental substances. Staining of the feathers with soil has been observed in a number of large birds and has universally been attributed to camouflage [34]; however, it has been most carefully studied in the rock ptarmigan (*lapogus mutus*). Both sexes sport all-white plumage at the start of the breeding season, as snow melts this becomes very conspicuous and females moult to produce feathers that appear to offer good camouflage. In contrast, males do not moult immediately but smear their feathers with soil before later moulting into a brown plumage [35]. The authors argue that the plumage soiling is unlikely to be a non-functional side-effect of dust bathing; since many birds dust-bathe without noticeable long-term soiling of their plumage. The responses of females, other males or predators to immaculate white versus soiled plumage has yet to be explored; nor is it clear why the behaviour is restricted to males.

Free-ranging adult bearded vultures (*Gypaetus barbatus*) typically have an orange colour on their underparts, neck and head conferred by iron oxide rich soils. Captive studies show that birds readily rub themselves in suitable soils. Colour tends to be greater in (socially-dominant) females than males, and increases progressively from juveniles, to immatures, to sub-adults to adults. This caused Negro et al. [36] to interpret the red colouration as a status signal. They argue that sites where such soils are available will be rare, with substantial costs associated with finding them and gaining access to them in intraspecific contests. The status-signalling interpretation was challenged by Arlettaz et al. [37], who suggested that the main function was medicinal: providing protection against bacteria, mobilising vitamin A and having anti-oxidant properties. The two functions are not incompatible, and our understanding of the signalling function would be aided by observation of the influence of staining on within-species interactions.

Many large ungulates wallow in muddy pools and this can leave a covering of dried mud on them afterwards. Such bathing has been suggested to aid thermoregulation, reduce parasite loads and disinfect wounds, but these suggested benefits have not been studied in any depth nor has a residual benefit to the resulting dried mud covering been explored. Most extensive study has been in wild boar (*Sus scrofa*) [38]. A number of mammals have been observed to apply environmental materials to their coat – often my rolling in material (reviewed in [39]). Hypothesised functions for this include protection from microbial pathogens, parasites and predators; but again these hypotheses have not generally been tested. For example, a number of rodents vulnerable to predation by snakes have been observed to apply parts of shed snake skins to their fur (e.g. [40]). This is assumed to cause the rodents to smell like their predators and hence be avoided by them, but reactions of snakes to for example taxidermic mounts treated to mimic the effects of this behaviour have not been reported.

Evidence of costs of decoration

Costs are often assumed to be vital for understanding the distribution of decorating taxonomically and ontologically, but have rarely been demonstrated. Herreid & Full [41] demonstrated that locomotion is more energetically expensive for shell-carrying hermit crabs than those without shells. Berke & Woodin [10] found that decoration increased weight-loss during starvation in spider crabs.

Olmstead & Denno [42] explored the cost of the shields (made from recycled waste) of the larvae of several species of tortoise beetles. In the laboratory, those with shields experimentally removed did not exhibit compensatory feeding to reconstruct the shield; nor did they show any benefit of reduction of costs in terms of survival, body mass or development time. Berke & Woodlin [43] put this lack of evidence of costs down to these larvae having a very slow-moving foraging style. In a field experiment where predators where excluded there was no effect of shield removal on development time, but those with a shield survived marginally less well (something the authors [40] suggested might be driven by desiccation). Bacher & Luder [44] similarly found no cost to experimental shield removal in the laboratory for a more mobile shield beetle *Cassida rubiginosa*; a result Berke & Woodin [43] suggested might be due to an ad libitum feeding regime. Bacher & Luder also found no cost in the field in terms of shields conferring greater ease of detection by predators or parasitoids; they tentatively suggest that shields might offer some camouflage against visual predators. In Caddisfly larvae, costs to rebuilding experimentally-removed cases have been shown in terms of smaller adult body size [45,46].

Conclusion

Decorating is a particularly diverse activity, and (like tool use) it is difficult to produce an unambiguous definition that covers all cases effectively. Nonetheless, we have offered a definition of decoration that should on the whole distinguish it from other phenomena and facilitate future work. Although decoration has been studied across many taxa, in all cases we have highlighted substantial limits to current understanding regarding both benefits and costs to such adaptations. Benefits are often assumed rather than demonstrated. Anti-predatory benefits are most commonly postulated, in contrast to humans where decoration functions strongly in social interactions. However, only in decorator crabs and cold-water urchins has the effectiveness of decorating in protection from predators been demonstrated in realistic encounters, including under field conditions. But even here the mechanism by which the anti-predatory benefit might be conferred remains unclear. It is generally assumed that the costs of decoration are the physical costs of transport while carrying the load of decorated material: this may explain the prevalence of decorating in aquatic organisms (where buoyancy reduces the cost of carrying a load) and small bodied taxa (where excess muscle power for load carrying is more available from scaling arguments of muscle cross section versus volume of carried material). This may also explain why in insects decoration seems to be confined to juveniles, since the weight of decorations would be problematic for flying adults. However, costs are rarely studied and even less rarely demonstrated. Costs associated with investment of time for example involved in gathering decorative material should also be given more consideration. Decorating is a varied and intriguing trait that has evolved on several occasions – it merits much more study.

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