

1 **The evolutionary ecology of decorating behaviour**

2 **Graeme D Ruxton¹ & Martin Stevens²**

3 **1. School of Biology, University of St Andrews, St Andrews KY16 9TH, UK**

4 **2. College of Life & Environmental Sciences, University of Exeter, Penryn Campus, Penryn,**
5 **Cornwall, TR10 9FE, UK**

6

7 **Abstract**

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

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

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23 Introduction

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

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

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

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

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

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

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

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

66 **Decorator crabs**

67 The most widely studied group of decorators are crabs of the superfamily *Majoidea*. The group has
68 over 900 species, about 75% of which show decorating over some or all of their body, having
69 specialised hooked setae to attach material from the environment. The adaptive value of this
70 decorating seems to be anti-predatory. Although such benefits to decorating are often postulated,
71 this is an unusual case where anti-predator benefits have been demonstrated against free-living

72 predators in the natural environment. Several studies [3-5] have found that experimentally altering
73 or removing decoration increased vulnerability to predators. In the laboratory, Thanh et al. [6] found
74 that in the presence of a perceived predatory threat there was a decrease in decorating with
75 increased presence of competitively dominant crabs, with this effect being stronger in juveniles than
76 adults. The authors interpreted this as suggestive that juveniles were more at risk of predation than
77 adults, and that perceived predatory risk induced increased aggression related to competition for
78 decorating materials. In support of this, the extent of decorating material on an individual was a
79 good predictor of dominance in aggressive encounters. Stachowicz and Hay [3] found no effect of
80 perceived predation risk on decorating. These authors argued that decoration required hours of
81 activity (which might heighten exposure to predators), and so one would not expect to see variation
82 in decoration in response to shorter-term fluctuations in perceived predation risk.

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

95 It would seem useful to further explore the behaviour of such crabs under enhanced predation risk
96 (for instance, olfactory cues of predatory fish) in a laboratory setting. If the primary defensive

97 function is camouflage, then we might expect (for example) movement away from the source of the
98 olfactory cues, reduced movement, hiding in physical structures, or changed substrate choice. Given
99 our understanding of crypsis by background matching and by disruptive camouflage [8], It should
100 also be possible to analyse images of crabs on preferred substrates to determine whether their
101 match to the background is enhanced post-decoration and through what mechanisms.

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

109 **Other aquatic organisms**

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

116 Dayton et al. [12] provide another rare demonstration of an anti-predator function under field
117 conditions. In staged encounters, Antarctic sea urchins decorated with hydroids were protected
118 from attack by anemones, but were invariably killed in a repeat encounter after the hydroids had
119 been removed. McClintock & Janssen [13] studied a pelagic Antarctic amphipod that often carries a
120 gastropod. In laboratory experiments they found that amphipods actively captured the gastropod

121 and that carrying behaviour offered protection against predatory fish. Ross [14] demonstrated in the
122 laboratory that octopus failed in attacks on hermit crabs carrying a sea anemone on their shell, with
123 previous work demonstrating that the crabs actively transfer anemones onto themselves.

124 Subsequently, a number of studies have demonstrated that hermit crabs obtain anti-predator
125 protection from sea anemones and hydroids on their shell ([15]), but evidence of active facilitation
126 of such association is often absent.

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

143 The larvae of many caddisfly (insect order Trichoptera) construct cases out of various environmental
144 materials bound together with silk. These cases are carried around, and even when feeding or
145 moving most of the organism remains inside the case. Cases offer physical protection from predators

146 in staged encounters in the laboratory [19,20], and may also function to reduce danger through
147 being swept from the substrate in lotic environments [21].

148 **Terrestrial species**

149 Larvae of a wide range of insects carry so-called “shields” of material [22]. Faecal material is a
150 prominent feature of these shields. The larvae drop their exuviae after each moult, but in many
151 cases collect them (together with their faeces) on two spines at their abdominal tip. It is widely
152 believed that the primary function of this shield is anti-predatory and/or anti-parasitoid, and there is
153 experimental support for this in the laboratory by Bacher & Luder [23]. They conducted field
154 experiments showing the shield of their focal species offered no effective defence against the main
155 predator (a paper wasp), but was highly effective defence against parasitoid wasps. They found no
156 protection against UV-B in the laboratory. A number of studies also demonstrated a protective
157 function against at least some predators in the laboratory [24]. Sometimes the protection appears
158 physical in nature, preventing predators with short mouthparts from being able to contact the larva
159 [25]. There is also evidence of chemical protection, with shield protection being diminished if it
160 remains physically intact but chemically changed either by solvent-leaching or by manipulation of
161 larval diet [26]. Nakhira & Arakawa [27] demonstrated that the “trash-package” of juvenile lacewing
162 *Mallada desjardinsi* reduced both the likelihood that ladybirds that encountered a lacewing would
163 attack it, and the probability that such an attack was successful; offering both crypsis and a physical
164 defence. Larvae of the green lacewing *Chrysopa slossonae* prey on the woolly alder aphid *Prociphilus*
165 *tesselatus*. A larva actively transfers waxy wool from the bodies of captured prey and places them on
166 its own body. Eisner et al. [28] demonstrated that this decoration provides defence against the ants
167 that tend the aphids: experimentally denuded larvae were seized and removed by ants, whereas
168 intact larvae were apparently unrecognised and left untouched.

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

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

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

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

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

216 Free-ranging adult bearded vultures (*Gypaetus barbatus*) typically have an orange colour on their
217 underparts, neck and head conferred by iron oxide rich soils. Captive studies show that birds readily
218 rub themselves in suitable soils. Colour tends to be greater in (socially-dominant) females than
219 males, and increases progressively from juveniles, to immatures, to sub-adults to adults. This caused
220 Negro et al. [36] to interpret the red colouration as a status signal. They argue that sites where such

221 soils are available will be rare, with substantial costs associated with finding them and gaining access
222 to them in intraspecific contests. The status-signalling interpretation was challenged by Arlettaz et
223 al. [37], who suggested that the main function was medicinal: providing protection against bacteria,
224 mobilising vitamin A and having anti-oxidant properties. The two functions are not incompatible,
225 and our understanding of the signalling function would be aided by observation of the influence of
226 staining on within-species interactions.

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

239

240 **Evidence of costs of decoration**

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

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

259 **Conclusion**

260 Decorating is a particularly diverse activity, and (like tool use) it is difficult to produce an
261 unambiguous definition that covers all cases effectively. Nonetheless, we have offered a definition
262 of decoration that should on the whole distinguish it from other phenomena and facilitate future
263 work. Although decoration has been studied across many taxa, in all cases we have highlighted
264 substantial limits to current understanding regarding both benefits and costs to such adaptations.
265 Benefits are often assumed rather than demonstrated. Anti-predatory benefits are most commonly
266 postulated, in contrast to humans where decoration functions strongly in social interactions.
267 However, only in decorator crabs and cold-water urchins has the effectiveness of decorating in
268 protection from predators been demonstrated in realistic encounters, including under field
269 conditions. But even here the mechanism by which the anti-predatory benefit might be conferred

270 remains unclear. It is generally assumed that the costs of decoration are the physical costs of
271 transport while carrying the load of decorated material: this may explain the prevalence of
272 decorating in aquatic organisms (where buoyancy reduces the cost of carrying a load) and small
273 bodied taxa (where excess muscle power for load carrying is more available from scaling arguments
274 of muscle cross section versus volume of carried material). This may also explain why in insects
275 decoration seems to be confined to juveniles, since the weight of decorations would be problematic
276 for flying adults. However, costs are rarely studied and even less rarely demonstrated. Costs
277 associated with investment of time for example involved in gathering decorative material should
278 also be given more consideration. Decorating is a varied and intriguing trait that has evolved on
279 several occasions – it merits much more study.

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