

## 12 Camouflage in decorator crabs

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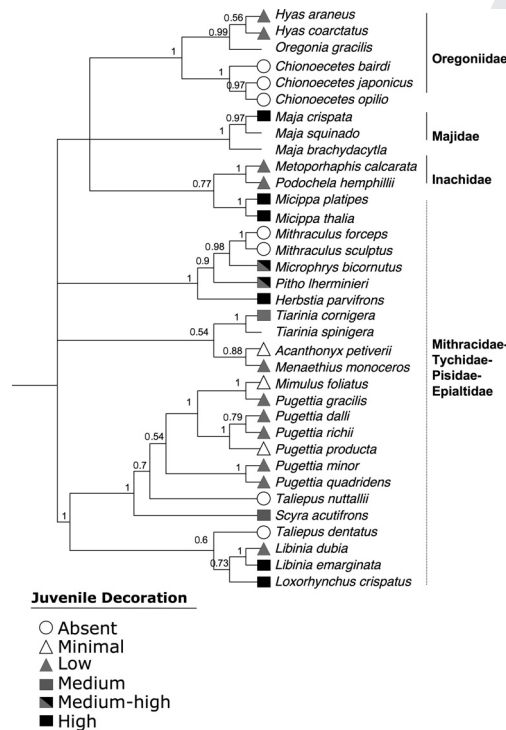
### Integrating ecological, behavioural and evolutionary approaches

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#### 12.1 Introduction

Camouflage is one of the most common anti-predator strategies in the animal kingdom, and many examples of camouflage have become classic case studies of adaptation and natural selection (Cott 1940; Kettlewell 1955; Stevens and Merilaita, 2009). Although most examples of animal camouflage involve body coloration or patterning, decorator crabs in the brachyuran superfamily Majoidea (majoids) are a large and diverse group of crabs best known for a distinctive form of ‘decoration’ camouflage, in which they attach materials from the environment to specialised hooked setae on their body. This unique form of camouflage is dependent both on crab morphology and behaviour, and makes decorator crabs an ideal group in which to study the adaptive consequences and mechanistic bases of camouflage. Decorator crabs are also fairly unusual among camouflaged animals in that the adaptive anti-predatory consequences of decoration camouflage have in many cases been directly tested in the field (Stachowicz and Hay, 1999b; Thanh *et al.* 2003; Hultgren and Stachowicz, 2008a). Yet despite its clear adaptive value, decoration camouflage varies widely across the majoids – both within and between species. Many majoids exhibit intra- and interspecific decreases in decoration with size (Dudgeon 1980; Wicksten 1993; Stachowicz and Hay, 1999b; Berke and Woodin, 2008; Hultgren and Stachowicz, 2009). Along with experimental work documenting energetic costs of carrying decoration (Berke and Woodin, 2008), and trade-offs with other forms of defence (Hultgren and Stachowicz 2008a), these data suggest that cost–benefit trade-offs may drive the evolution of decoration in these crabs (Hultgren and Stachowicz, 2009). These results more broadly imply that the value of camouflage as a concealment strategy is strongly influenced by constraints such as body size, providing predictions to be tested in other groups of organisms.

The experimental tractability of decorator crabs and their willingness to redecorate readily in the laboratory, combined with an increasingly robust understanding of their phylogenetic relationships, provide grist for hypothesis testing about the origins and function of decoration itself and of camouflage strategies in general (Hultgren and Stachowicz, 2008b, 2009; Hultgren *et al.*, 2009). In this chapter, we review decoration in the majoid crabs, discuss evidence for the adaptive functions of decoration, and



**Figure 12.1** Phylogenetic tree of the Majoidea (Bayesian consensus tree, species names and trees modified from Hultgren and Stachowicz 2009). Numbers above each node indicate Bayesian posterior probabilities for that clade; icons mapped to terminal taxa indicate juvenile decoration category groupings (decoration data is not available for species lacking icons). Names in bold indicate clades that map to single families (solid lines) or multiple families (dashed lines).

explore how these crabs can contribute to our general understanding of the ecology and evolution of camouflage.

## 12.2 Decoration as a morphological and behavioural trait

### 12.2.1 Morphological components of decoration behaviour

While decorating behaviour has been observed in nearly 25% of major metazoan phyla (Berke *et al.* 2006), it is most widespread and well developed in the decorator crabs from the crustacean superfamily Majoidea. The majoids are a diverse group of over 900 species worldwide (Rathbun 1925; Wicksten 1993; De Grave *et al.* 2009), which is estimated to have diverged from the rest of the Brachyura ~200 million years ago (Porter *et al.* 2005). Majoids have evolved a specific adaptation to facilitate decoration – Velcro-like, hooked setae on their carapace that they use to fasten materials from their environment to their body. Phylogenetic evidence suggests that species at the base of the majoid tree possess hooked setae and actively decorate (Hultgren and Stachowicz, 2008b) (Figure 12.1), and preliminary estimates suggest that ~75% of all majoids

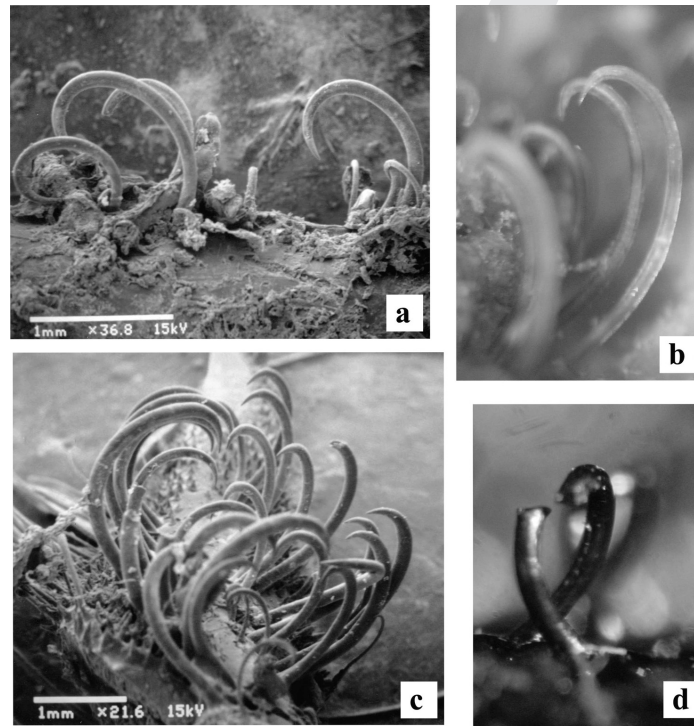
(including members of all eight families) decorate at least part of their carapace during some phase of their life (Hultgren and Stachowicz, 2009).

Some of the first observations of decoration behaviour in majoid crabs came from Aurivillius (1889), who observed that crabs manipulated decoration materials in their mouths before attaching them, and hypothesised that the crabs secreted some type of adhesive from their mouthparts to attach decoration materials to their carapace. A series of experiments (Wicksten 1977, 1978, 1979) ablating either hooked setae or mouthparts of crabs demonstrated that crabs primarily attached decoration using hooked setae, confirming earlier observations by Rathbun (1925) that crabs passed material through their mouth to soften the ends for decorating. Decoration behaviour is thus strongly linked to morphology; the more hooks a crab has, the more it can decorate. Across many species there is a positive correlation between area of the carapace covered with hooked setae and area covered by decoration ( $R^2 = 0.91$ ), suggesting hook cover is a quantitative proxy for the potential to decorate in the field (Hultgren and Stachowicz 2009).

Majoid crabs produce several different types of hooked setae (Wicksten 1976; Szebeni and Hartnoll, 2005; Rorandelli *et al.* 2007; Berke and Woodin 2009). Hooked setae (also known as curved setae) have a relatively long shaft with a curved distal region (Figure 12.2), and are one of the most common types of setae seen on crabs. Their structural similarity to Velcro (Figure 12.2) is remarkable and provides a convenient analogy for how decoration is held in place. ‘Bent’ setae are shorter and more acutely bent than hooked setae, and also function in decoration (Szebeni and Hartnoll, 2005). Straight, or ‘pappose’, setae are typically straighter and distally tapered, and often covered with small setules; these and other non-hooked setae have been hypothesised to play a sensory role in informing the crab of the status of its decoration (Wicksten 1993; Berke and Woodin 2009). This diversity of setal forms appears to serve some function in attaching a wide range of decoration materials; Rorandelli *et al.* (2007) found setae from different parts of the body in the crab *Inachus phalangium* differed in morphology and corresponded to the different decoration types used on these areas of the body.

### 12.2.2 Behavioural aspects of decorating

Despite being morphologically constrained by hook cover, the actual amount of decoration on the carapace and its composition is behaviourally determined (Stachowicz and Hay, 1999b; Thanh *et al.* 2003, 2005). We briefly introduce behavioural influences on decoration here, then elaborate on these in the section on adaptive significance of decoration. The default assumption is often that majoids are generalists, decorating with materials in rough proportion to their availability in the environment (Kilar and Lou, 1984; Wicksten 1993; Fürböck and Patzner, 2005; Martinelli *et al.* 2006). This strategy should allow crabs to achieve crypsis via background matching (Endler 1978). However, many crabs exhibit distinct decoration preferences (Table 12.1). While some crabs prefer to decorate with the same decoration materials they consume for food (Wicksten 1993; Woods and McLay, 1994a, 1994b), the majority of crabs in which food and decoration preferences have been studied prefer to feed on and decorate with different materials. In particular, many crabs preferentially utilise chemically defended plants or sessile



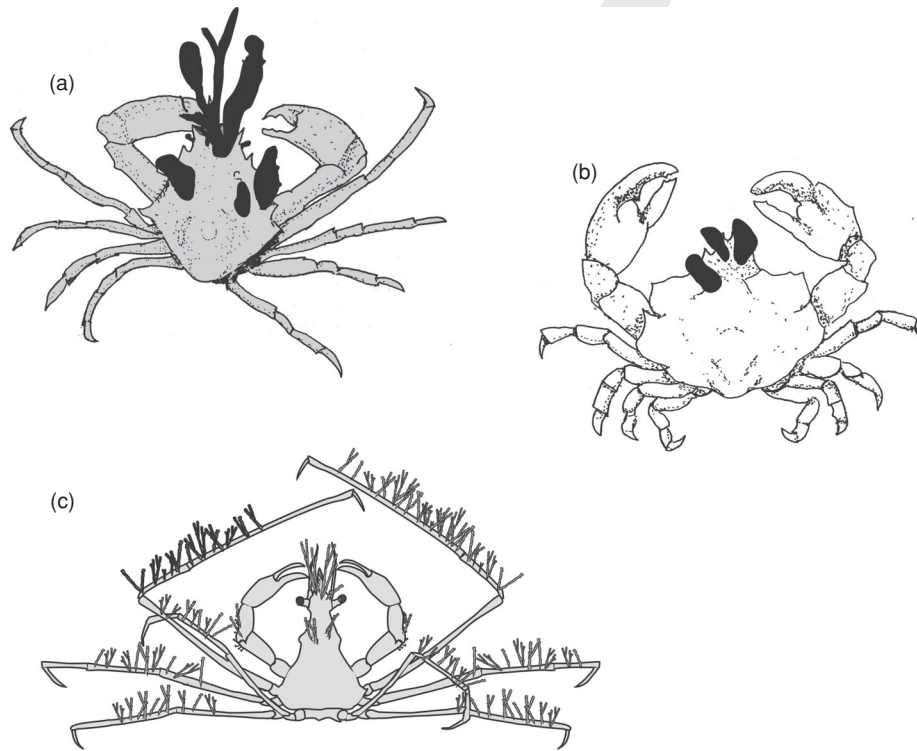
**Figure 12.2** Hooked setae used to hold decoration in majoid crabs (a–c) compared to man-made Velcro (d). (a) Scanning electron photograph of setae from the leg of *Oregonia gracilis*; (b) dissecting microscope photograph of setae from the carapace of *Loxorhynchus crispatus*; (c) scanning electron photograph of setae on the rostrum of *Pugettia richii*; (d) dissecting microscope photograph of man-made Velcro. For (a) and (c), white lines indicate scale bars.

animals for decoration (summarized in Table 12.1; see also Section 12.3). Several species prefer to decorate with materials that appear morphologically easier to handle (which could reduce the time needed for decoration), such as thin branched algae (Fürböck and Patzner, 2005; Hultgren *et al.* 2006), or younger forms that are easier to cut (Woods and McLay, 1994b).

Behavioural choice of decoration is often complemented by other activities that might enhance the effectiveness of decoration as camouflage. Majoids are typically immobile during the day and freeze upon approach by predators (Wirtz and Diesel, 1983; Kilar and Lou, 1984; Wicksten 1993), and some increase decoration in the presence of predators (Thanh *et al.* 2003). Habitat selection behaviour – choosing habitats that match their camouflage, or adjusting camouflage to match their habitat – is also a crucial behaviour mediating the effectiveness of camouflage; organisms living in patchy environments may be limited to patches or habitats where their camouflage most closely matches the background (Cott 1940; Merilaita *et al.* 1999). However, few studies have been done on this topic in decorator crabs, and results are equivocal, with some crabs adjusting their camouflage based on environment (Wilson 1987) and others failing to do so (Getty and Hazlett, 1978).

**Table 12.1** Prevalence of specialized decoration preferences in majoid crabs. An asterisk (\*) indicate studies in which preference was experimentally quantified in the laboratory or the field

Family	Genus	Species	Reference	Specialised decoration preference
Inachidae	<i>Inachus</i>	<i>aguiarii</i>	Maldonado and Uriz, 1992	Prefers to decorate with sponges
	<i>Inachus</i>	<i>phalangium</i>	Rorandelli <i>et al.</i> , 2007	Preferentially uses the chemically noxious alga <i>Dictyota dichotoma</i> in areas of its body most exposed to predators*
Majidae	<i>Macropodia</i>	<i>rostrata</i>	Cruz-Rivera, 2001	Specialises on the chemically defended algae <i>Dictyota linearis</i> *
	<i>Notomithrax</i>	<i>ursus</i>	Woods and McLay, 1994a, 1994b	Prefers to decorate with same materials used for food*
	<i>Thacanophrys</i>	<i>filholi</i>	Woods and Page, 1999	Prefers to decorate with chemically noxious sponges in laboratory*
Mithracidae	<i>Micippa</i>	<i>platipes</i>	Hultgren <i>et al.</i> , 2006	Specialises on algae <i>Hypnea pannosa</i> in some locations*
	<i>Microphrys</i>	<i>bicornutus</i>	Kilar and Lou, 1986	Prefers to decorate with same materials used for food*
	<i>Stenocionops</i>	<i>furcata</i>	Cutress <i>et al.</i> , 1970	Prefentially attaches stinging anemone <i>Calliactis tricolor</i> to carapace
Pisidae	<i>Herbstia</i>	<i>parvifrons</i>	K. Hultgren, unpublished	Decorates only with sponges; sponges provide some form of chemical or morphological defence
	<i>Libinia</i>	<i>dubia</i>	Stachowicz and Hay, 1999b	Specialises on the chemically defended algae <i>Dictyota menstrualis</i> in some locations*
Libinia	<i>Libinia</i>	<i>spinosa</i>	Boschi, 1964; Acuna <i>et al.</i> , 2003	Uses the anemone <i>Antholoba achates</i> as decoration (can be temporary)
	<i>Loxorhynchus</i>	<i>crispatus</i>	K. Hultgren, unpublished	Prefentially decorates with the bryozoan <i>Bugula neritina</i> (chemically defended in some areas)
Loxorhynchus	<i>Loxorhynchus</i>	spp.	Wicksten, 1993	Occasionally decorates with stinging anemone <i>Corynactis californicus</i>
	<i>Pelta</i>	<i>tumida</i>	Wicksten, 1993; K. Hultgren unpublished	Decorates only with sponges; sponges provide some form of chemical or morphological defence



**Figure 12.3** The epialtid kelp crabs *Pugettia richii* (a) and *Mimulus foliatus* (b) decorate minimally, but change colour to match the colour of their algal habitats. The inachid crab *Podochela hemphilli* (c) decorates little of its carapace, but unlike many majoids covers its chelae and walking legs extensively with decoration such as branched bryozoans.

### 12.2.3 Other forms of camouflage

Decoration has been lost many times throughout the evolution of the majoid crabs (Hultgren and Stachowicz 2008b, 2009), and non-decorating majoids typically possess other anti-predator behaviours such as cryptic coloration or association with structurally or chemically defended sessile organisms. Many species with minimal decoration adopt other forms of flexible camouflage, such as changing the colour of their carapace by sequestering pigments from algae they live on and consume in a form of camouflage (Plate 1e, Figure 12.3a, b)(Hines 1982; Wilson, 1987; Iampietro 1999; Hultgren and Stachowicz, 2008a). For example, in California *Pugettia producta* (Plate 1e) lives in intertidal red algae as a juvenile and migrates to amber-coloured kelp forests as an adult, changing colour from red to amber in the process (Hines 1982; Hultgren and Stachowicz, 2010). Colour change only occurs when crabs moult (every 3–6 weeks as a juvenile), and is clearly linked to algal pigments in the diet (Wilson 1987; Iampietro 1999). Natural history accounts suggests colour change may be widespread among the Epialtidae, or ‘kelp crabs’ (Table 12.2)(Brusca 1980; Wu *et al.* 1999; Cruz-Rivera 2001; Vasconcelos *et al.* 2009), and epialtids readily change colour in the laboratory

**Table 12.2** Reported examples of colour camouflage in majoid crabs (family Epialtidae)

Genus	Species	Reference	Location	Notes
<i>Acanthonyx</i>	<i>formosa</i>	Wu <i>et al.</i> , 1999	Taiwan	Crab carapace colour varies with colour of algal habitats (green, brown or black algae)
<i>Acanthonyx</i>	<i>lunulatus</i>	Cruz-Rivera, 2001	Mediterranean	Crab colour matched the colour of their algal habitat
<i>Acanthonyx</i>	<i>petiverii</i>	Wilson, 1987	Chile	Colour of carapace matches with colour of algal habitats; crabs fed algae in the laboratory changed colour
<i>Acanthonyx</i>	<i>scutiformis</i>	Vasconcelos <i>et al.</i> , 2009	Brazil	Crabs actively changed colour when fed algae in the laboratory
<i>Epialtus</i>	<i>minimus</i>	Brusca, 1980	Mexico (Gulf of California)	Colour of carapace matches colour of intertidal algal habitat ( <i>Sargassum</i> sp.)
<i>Huenia</i>	<i>heraldica</i>	Wicksten, 1983	Australia	Colour of carapace matches colour of algal habitat ( <i>Halimeda</i> sp.)
<i>Mimulus</i>	<i>foliatus</i>	Hultgren and Stachowicz, 2008a	USA (Pacific coast)	Crabs actively change colour in the field and laboratory to match algal habitats
<i>Pugettia</i>	<i>dalli</i>	Hultgren and Stachowicz, 2009	USA (Pacific coast)	Crabs actively change colour in the field and laboratory to match algal habitats
<i>Pugettia</i>	<i>gracilis</i>	Hultgren and Stachowicz, 2009	USA (Pacific coast)	Crabs actively change colour in the field and laboratory to match algal habitats
<i>Pugettia</i>	<i>producta</i>	Hultgren and Stachowicz, 2008a	USA (Pacific coast)	Crabs actively change colour in the field and laboratory to match algal habitats
<i>Pugettia</i>	<i>quadridentis</i>	K. Hultgren, unpublished	Japan	Colour of carapace matches colour of algal habitats
<i>Pugettia</i>	<i>richii</i>	Hultgren and Stachowicz, 2008a	USA (Pacific coast)	Crabs actively change colour in the field and laboratory to match algal habitats
<i>Simocarcinus</i>	<i>simplex</i>	Wicksten, 1983	Hawaii	Colour of carapace matches colour of intertidal algae habitat ( <i>Sargassum</i> sp.)

when fed different-colored algae (Wilson 1987; Hultgren and Stachowicz, 2008a). As some colour-changing species shift between discrete, different-coloured algal habitats, appropriate habitat selection appears to be crucial in mediating the effectiveness of colour camouflage (Hultgren and Stachowicz, 2008a, 2010).

In some cases, crabs more permanently mimic both the coloration and the morphology of a particular host plant in a form of masquerade, presumably leading to a near-obligate specialisation (Wicksten 1983; Griffin & Tranter 1986; Hay *et al.* 1990; Goh *et al.* 1999; Tazioli *et al.* 2007). As one spectacular example, the tropical Pacific crab *Huenia heraldica* has carapace projections and coloration that strongly resembles its host algae in the genus *Halimeda* (Wicksten, 1983) (Plate 1c).

## 12.3 Adaptive value of decoration

### 12.3.1 Decoration as an anti-predator adaptation

Decoration can function as an anti-predator behaviour by either reducing the probability of detection (a pre-detection defence), or by reducing the probability of recognition or the probability of consumption once a crab is detected (post-detection defences). Decorator crabs avoid detection by background matching, matching a specific object (masquerade), or by decorating in a way that breaks up the outline of the crab body (a form of disruptive camouflage). Many crabs decorate with noxious plants or animals; in this case, predators may detect the crab but ignore it because it is recognised to be distasteful, or attempt to consume it but are deterred by noxious decorations (Wicksten 1980; Stachowicz and Hay 1999b). Below we review the direct and indirect evidence supporting the anti-predator function of decoration.

#### 12.3.1.1 Direct evidence

Several studies have tethered crabs in the field with decoration altered or intact, and all have found evidence that intact decoration increases crab survival (Stachowicz and Hay, 1999b; Thanh *et al.*, 2003; Hultgren and Stachowicz, 2008a). Numerous anecdotal observations also support the anti-predator function of decoration. For example, Wicksten (1980, 1993) noted that octopuses in tanks ignored decorated crabs while consuming crabs of non-decorator species, and predatory fish in aquaria and in the field recognised and captured well-decorated crabs but promptly spat them out. This suggests, that for some species, decoration materials may make the crab either chemically noxious, or simply smell (or taste) like something other than a crab – the latter possibly suggesting a role for decoration as non-visual crypsis (Chapter 17).

#### 12.3.1.2 Preferential use of noxious or unpalatable decoration materials

Field surveys that rigorously quantify availability and utilisation of decoration materials, as well as controlled laboratory experiments, have demonstrated that many decorator crabs are quite selective decorators (Stachowicz and Hay, 1999b; Woods and Page, 1999; Cruz-Rivera, 2001; Hultgren *et al.*, 2006). In several of these cases, crabs preferentially



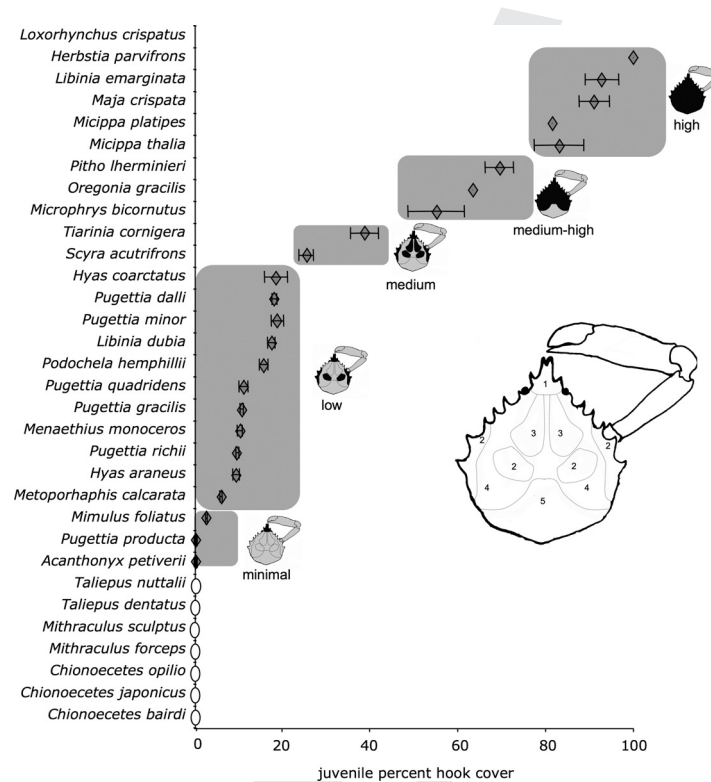
decorate with chemically noxious seaweeds, sponges or other invertebrates that might provide them a chemical refuge from predators. For example, *Libinia dubia* (Plate 1f) decorates almost exclusively with the brown seaweed *Dictyota menstrualis*, which produces several diterpene alcohols that make it unpalatable to fishes. Because these fishes also consume small invertebrates like crabs, *Dictyota* serves as an ideal camouflage material for the carapaces of these crabs, and crabs decorated in this way experience much less predation than crabs decorated with algae that fishes like to eat (Stachowicz and Hay 1999b). *Libinia*'s strong preference for decorating with *Dictyota* is cued proximally by the presence of a single chemical compound, dictyol E. Because this compound is the one that is responsible for deterring predators in *Dictyota*, the crabs are, in effect, behaviourally sequestering the defensive compounds present in the alga by using them as decoration (Stachowicz and Hay 1999b).

Although it has not been as rigorously demonstrated in other systems, much evidence suggests this behaviour is widespread (Table 12.1): several European decorator crabs (*Macropodia rostrata* and *Inachus phalangium*) preferentially decorate with other chemically noxious *Dictyota* species (Cruz-Rivera, 2001; Rorandelli *et al.*, 2007) that also produce dictyol E. Many majoids preferentially decorate with sponges (Sanchez-Vargas and Hendrickx, 1987; Maldonado and Uriz, 1992; Wicksten, 1993; Woods and Page, 1999), and in at least two cases (*Pelia tumida* and *Herbstia parvifrons*) sponge decorations appear to deter some feeding by predatory fish (K. Hultgren unpublished data). *Loxorhynchus crispatus* selectively decorates with chemically noxious bryozoans (K. Hultgren and J. Stachowicz unpublished data) that have been shown by others to deter predation by fishes (Lopanik *et al.*, 2006). Several other species decorate with anemones, which have stinging nematocysts that may deter crab predators (Boschi, 1964; Cutress *et al.*, 1970; Acuna *et al.*, 2003).

The wide distribution of this trait, with no apparent phylogenetic signal (Hultgren and Stachowicz 2009), suggests that decorating with noxious or unpalatable materials might easily arise many times simply by crabs placing items that are unpalatable to them on their carapace. The portable refuge that this provides (Stachowicz and Hay 1999b) could result in rapid selection for this behaviour.

### 12.3.1.3 Spatial distribution of decoration

Many majoids decorate only their rostrum, or decorate the rostrum first when decorating (Wicksten, 1979; Dudgeon, 1980; Mastro, 1981; Wicksten, 1993; Woods and McLay, 1994b; Hultgren and Stachowicz, 2009). Covering this part of the body conceals the antennae, which may move even when the rest of the body is still (Dudgeon 1980; Wicksten 1993). Crabs that only decorate their rostrum still have reduced rates of predation compared to crabs with decoration removed (Hultgren and Stachowicz 2008a), suggesting that even this minimal level of decoration has adaptive significance. More generally, comparative studies of decoration cover suggest that decoration cover varies among species in a distinctly nested fashion (Hultgren and Stachowicz, 2009) (Figure 12.4). For example, the most minimal decorators typically cover their rostrum, crabs with slightly higher cover decorate their rostrum and epibranchial areas, and species with increasingly higher decoration appear to 'add' decoration to sections of the carapace in a



**Figure 12.4** Mean juvenile hook cover and portions of the body covered for different majoid species (originally printed in Hultgren and Stachowicz 2009). Large crab illustration represents a generalized majoid, with portions of the body outlined in the order in which they were decorated (1 = rostrum; 2 = epibranchial areas and sides of the body; 3 = protogastric regions; 4 = mesobranchial areas; 5 = metabranchial and cardiac areas). In the graph, bars represent standard errors, and open ovals indicate non-decorators. Shaded areas indicate majors belonging to different categorical groupings of decoration, and crab diagrams indicate approximate portions of the body covered by decorators in each grouping. © 2009 *The American Naturalist*.

fixed order. Exceptions to this general rule often reflect the specific biology of the crab; for example, the anemone-dwelling crab *Inachus phalangium* has the most dense hooks and most concentrated decoration in the parts of the body (rostrum and front claws) that are most exposed to predation (Rorandelli *et al.*, 2007).

### 12.3.2 Other functions of decoration

#### 12.3.2.1 Food storage

The observation that some decorator crabs exhibit similar preferences for feeding and decoration (Mastro, 1981; Kilar and Lou, 1986; Woods and McLay, 1994a, 1994b; Sato and Wada, 2000) has led to the idea that the adaptive value of decoration for these species may be as a food cache (Woods and McLay, 1994b). When starved in the laboratory, many species will consume their decoration (Wicksten, 1980; Mastro, 1981; Wicksten,

1993), but there is little evidence that materials stored as decoration are actually used for food in the field. Even when decoration is consumed, it is usually a relatively small proportion of the total amount of decoration (Wilson, 1987; Woods and McLay, 1994b), and many species prefer different materials for feeding and decoration (e.g. Stachowicz and Hay 1999b; Sato and Wada 2000; Cruz-Rivera 2001). Using decoration as a short-term food storage could reduce predation risk if decorating with food items takes less time than consuming it *in situ*, allowing crabs to transport preferred food found in exposed areas to refuges for consumption. Some members of the Oregoniidae and Inachidae families of decorator crabs waft their legs through water (Berke and Woodin, 2009), in what Wicksten (1980) hypothesised is a method of capturing food, leading her to suggest that the origins of decoration may lie in food collection (these lineages are thought to have diverged early in the majoid tree), even if presently its main function is predation avoidance (Wicksten 1993). Recent molecular and morphological phylogenies fail to provide evidence in support of this hypothesis, as species that use decoration as camouflage from predators are not necessarily derived from lineages in which food storage is the primary function (Hultgren and Stachowicz, 2008b, 2009), though it is possible that such lineages are not sampled in the phylogeny or have gone extinct.

#### **12.3.2.2 Intraspecific signalling**

Many species do show sexual dimorphism in the quantity of decoration, but this has mostly been interpreted as a consequence of sexual dimorphism in claw size and the constraints associated with carrying the mass of both decoration and heavy claws, rather than intersexual communication (Berke and Woodin 2008; and see below). Others have suggested that the increase in apparent size of individuals as a result of decoration could increase the likelihood of submission in intraspecific encounters (Hazlett and Estabrook, 1974), though evidence is limited.

#### **12.3.2.3 Prey capture**

Concealment from potential prey could aid in ambush predation. One anecdotal report observed that heavily decorated lyre crabs (genus *Hyas*) stealthily approach and capture small crabs and fish in aquaria (Wicksten, 1980, 1983). However, the role of decoration camouflage in facilitating prey capture was not directly examined. Most decorator crabs are very slow and are not reported to feed on active prey, so we suspect this function is of minor importance. In cases in which crabs decorate extensively with structurally complex seaweeds or invertebrates that are colonised by smaller invertebrates like amphipods or polychaetes, it is possible that crabs might use decoration to attract food, but direct evidence of this is lacking.

### **12.4 Decorator crabs and the evolution of camouflage**

Comparing decoration behaviours (or lack thereof) among species or among populations within species has provided insights into the factors that shape these behaviours and select

for the evolution and maintenance of camouflage more generally. Intraspecific variation has been reported geographically, intersexually and ontogenetically, and been used to evaluate the forces selecting for and against specific camouflage behaviours in individual species. Comparisons across species have been facilitated by recent advances in our understanding of the phylogenetic relationships among the majoids (Marques and Pohle, 2003; Hultgren and Stachowicz, 2008b, 2009). Such comparisons have allowed rigorous tests of cost–benefit trade-offs, demonstrated the evolutionary lability of decoration, and provided insights into the forces driving the evolution of alternative camouflage tactics.

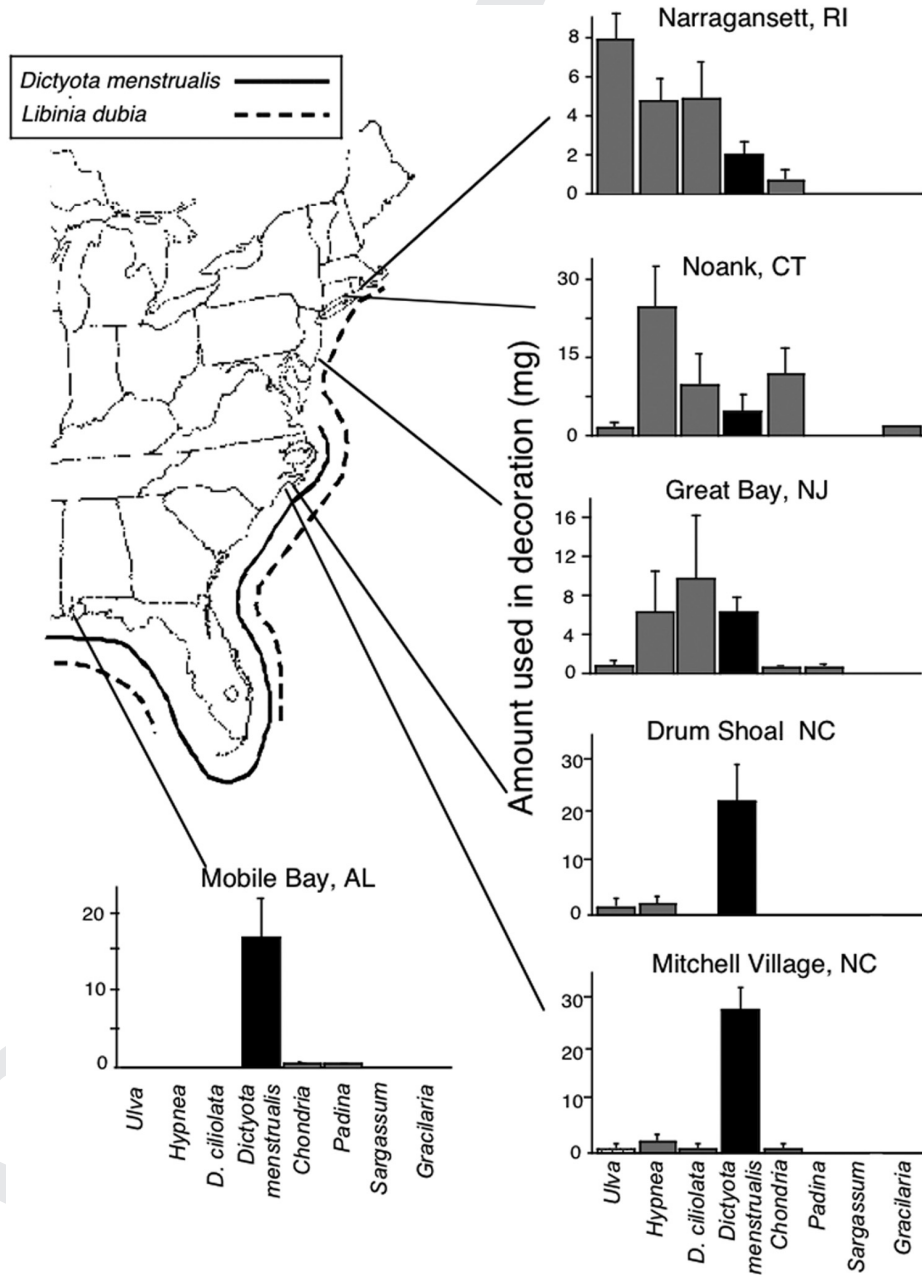
#### 12.4.1 Intraspecific variation

##### 12.4.1.1 Geographical variation and the evolution of specialisation

Geographical variation in the outcome of interspecific interactions is thought to be important to the evolution of specialization (Thompson, 1994). Comparisons among populations of decorator crabs, which can vary geographically in their preferences for different decoration materials (Stachowicz and Hay 2000; Hultgren *et al.* 2006), may help us further understand what drives variation in decoration specialisation. For example, generalist vs. specialist camouflage strategies (Merilaita *et al.*, 1999; Stachowicz and Hay, 2000) may be differentially effective against different types of predators in different regions. Several decorator crabs are more selective in acquiring decoration in lower-latitude locations (Stachowicz and Hay 2000; Hultgren *et al.* 2006), though this has been tested in only a few cases. The best-studied example of this is the majoid *Libinia dubia*, which exhibits strong specialization in decoration in southeastern USA, where it decorates almost exclusively with the chemically defended brown alga, *Dictyota menstrualis*. However, *Dictyota* is absent in the northern part of this crab's range (Figure 12.5), and crabs from these northern locations decorated to match their environment in both the field and the laboratory. In addition, in winter and spring, when *Dictyota* was seasonally absent in southern locations, *Libinia* selectively camouflaged with a chemically noxious sponge. Thus, southern crabs were consistent specialists on chemically defended species for camouflage, while northern crabs were more generalised (Figure 12.5). The geographical shift in crab behaviour away from specialisation coincides with a reported decrease in both total predation pressure and the frequency of omnivorous consumers that eat both seaweeds and crustaceans (references in Stachowicz and Hay 2000). These shifts in the nature and intensity of predation may favour different camouflage strategies (generalist vs. specialist), contributing to the observed geographical differences in camouflage behaviour. A similar latitudinal gradient in decoration selectivity was reported by Hultgren *et al.* (2006) for decorator crabs in Japan, although the mechanisms causing variation in decoration specialisation in this case are less clear.

##### 12.4.1.2 Intersexual and ontogenetic changes and the costs of camouflage

A key aspect of understanding constraints on the evolution of camouflage involves a better understanding of the costs of these behaviours. These probably include direct



**Figure 12.5** Use of North Carolina seaweeds for camouflage (mean + 1 s.e.) by *Libinia dubia* from six locations along the east coast of the United States (originally printed in Stachowicz and Hay, 2000). Black bars indicate utilization of *Dictyota menstrualis*, grey bars indicate utilization of other algae. The range of occurrence of *L. dubia* and *D. menstrualis* are given for comparison. © 2000 *The American Naturalist*.

costs involved with the time and energy required for collecting and placing decoration; in cases in which crabs are highly selective in their choice of decoration (Table 12.1), search costs might be substantial, though this has never been quantified. In addition to costs of the act of decoration itself, there are apparently energetic costs associated with carrying decoration, either in terms of the weight of the decoration itself, or increased drag forces experienced in flow (Berke and Woodin 2008). Together with studies demonstrating inter- and intraspecific variation in decoration with size and other factors, these data suggest cost–benefit trade-offs may have strong influences on the evolution of camouflage in the majoids.

Many species reduce decoration intensity with increased size, even ceasing altogether at adulthood, implying some cost associated with decoration (reviewed in Hultgren and Stachowicz 2009; Berke and Woodin 2009). Larger crabs are likely to be less susceptible to predation, especially against gape-limited predators such as fish (Stachowicz and Hay 1999b), and cryptic camouflage may be more effective for smaller animals (Cott 1940), so the benefits of decoration might decrease with size, with costs selecting for the loss of decoration in large adults. A number of species also exhibit sexual dimorphism in decoration loss, with adult males having greatly reduced decoration and setal densities relative to adult females or juveniles (Berke and Woodin, 2009). In these species males often have increased claw size at maturity relative to females, presumably as an adaptation to female choice or intrasexual competition for access to mates. Berke and Woodin (2008) argue that this represents evidence for a trade-off between investment in carrying decoration and carrying the mass of enlarged claws. They experimentally demonstrated that decorated individuals suffered greater energetic losses when starved than undecorated individuals – but only when allowed free movement – suggesting that the cost of locomotion was greater in decorated individuals. Artificial addition of claws and decoration to undecorated immature individuals resulted in dramatic weight loss, greater than either claws or decoration alone, suggesting that the costs of carrying decoration may be substantial. Even when the weight of decoration is minimal, increased drag forces on the crab in flow could still impose costs. Many crabs decorate with large pieces of algae or hydroids that project from the body surface (Figure 12.3a) that could hinder locomotion in flow.

#### 12.4.2 Interspecific variation: phylogenetic approaches

Phylogenetic comparative methods are important tools in examining the evolution of camouflage, including understanding why species use different types of adaptive coloration (e.g. crypsis vs. mimicry), and which ecological or morphological factors shape the evolution of concealment strategies (Ruxton *et al.*, 2004). Most phylogenetically controlled comparative studies of adaptive animal coloration have focussed on the evolution of aposematic coloration (Tullberg and Hunter, 1996; Summers and Clough, 2001; Hagman and Forsman, 2003; Nilsson and Forsman, 2003), while relatively few have examined the evolution of cryptic body coloration or camouflage from a phylogenetic perspective (Ortolani, 1999; Stoner *et al.*, 2003).

**Table 12.3** Majoid species in which intraspecific variation in decoration have been examined. For type of study, a = tested for ontogenetic decreases in setal hook or decoration cover, b = tested for ontogenetic variation in setal morphology, c = anecdotal studies documenting ontogenetic variation in decoration, and d = tested for sexually dimorphic ontogenetic variation in setal morphology and/or hook cover. Some species are listed twice (e.g., if they showed ontogenetic variation in setal hook cover but not in setal hook density)

Family	Genus	Species	Type of study	Reference
Majoid species with an ontogenetic shift in decoration				
Epialtidae	<i>Pugettia</i>	<i>gracilis</i>	a	Hultgren and Stachowicz, 2009
	<i>Pugettia</i>	<i>producta</i>	a	Berke and Woodin, 2008; Hultgren and Stachowicz, 2009
Inachidae	<i>Eurypodius</i>	<i>laterillei</i>	d	Berke and Woodin, 2008
	<i>Macrocheira</i>	<i>kaempferi</i>	c	Wicksten, 1993
Majidae	<i>Metoporphaphis</i>	<i>calcarata</i>	a	Hultgren and Stachowicz, 2009
	<i>Maiopsis</i>	<i>panamensis</i>	b	Berke and Woodin, 2008
	<i>Maja</i>	<i>squinado</i>	b, c	Berke and Woodin 2008; Parapar <i>et al.</i> 1997
Mithracidae	<i>Micippa</i>	<i>platipes</i>	a	Hultgren and Stachowicz, 2009
	<i>Microphrys</i>	<i>bicornutus</i>	a	Hultgren and Stachowicz, 2009
	<i>Stenocionops</i>	<i>furcatus</i>	b	Berke and Woodin, 2008
	<i>Tiarinia</i>	<i>cornigera</i>	a	Hultgren and Stachowicz, 2009
Oregoniidae	<i>Hyas</i>	<i>araneus</i>	a, d	Berke and Woodin, 2008; Hultgren and Stachowicz, 2009
	<i>Hyas</i>	<i>coarctatus</i>	a	Hultgren and Stachowicz, 2009
	<i>Oregonia</i>	<i>bifurcata</i>	d	Berke and Woodin, 2008
	<i>Oregonia</i>	<i>gracilis</i>	d	Berke and Woodin, 2008; Hultgren and Stachowicz, 2009
Pisidae	<i>Chorillia</i>	<i>longipes</i>	d	Berke and Woodin, 2008
	<i>Libinia</i>	<i>dubia</i>	a	Berke and Woodin, 2008; Stachowicz and Hay, 1999; Hultgren and Stachowicz, 2009
	<i>Libinia</i>	<i>emarginata</i>	a, b	Berke and Woodin, 2008; Hultgren and Stachowicz, 2009
	<i>Loxorhynchus</i>	<i>grandis</i>	b, c	Wicksten, 1979; Berke and Woodin, 2008
	<i>Loxorhynchus</i>	<i>crispatus</i>	a, d, c	Wicksten, 1979; Berke and Woodin, 2008; Hultgren and Stachowicz, 2009
	<i>Pisa</i>	<i>tetraodon</i>	d	Berke and Woodin, 2008
Tychidae	<i>Pitho</i>	<i>lherminieri</i>	a	Hultgren and Stachowicz, 2009
Majoid species with no ontogenetic shift in decoration				
Epialtidae	<i>Menaethius</i>	<i>monoceros</i>	a	Hultgren and Stachowicz, 2009
	<i>Mimulus</i>	<i>foliatus</i>	a	Hultgren and Stachowicz, 2009
	<i>Pugettia</i>	<i>dalli</i>	a	Hultgren and Stachowicz, 2009
	<i>Pugettia</i>	<i>gracilis</i>	b	Berke and Woodin, 2008
	<i>Pugettia</i>	<i>minor</i>	a	Hultgren and Stachowicz, 2009
	<i>Pugettia</i>	<i>quadridens</i>	a	Hultgren and Stachowicz, 2009
	<i>Pugettia</i>	<i>richii</i>	c, a	Hultgren and Stachowicz, 2009

**Table 12.3** (cont.)

Family	Genus	Species	Type of study	Reference
Inachidae	<i>Achaeus</i>	<i>japonicus</i>	b	Berke and Woodin, 2008
	<i>Achaeus</i>	<i>stenorhynchus</i>	b	Berke and Woodin, 2008
	<i>Podochela</i>	<i>curvirostris</i>	b	Berke and Woodin, 2008
	<i>Podochela</i>	<i>hemphillii</i>	c, a	Hultgren and Stachowicz, 2009
	<i>Podochela</i>	<i>sydneyi</i>	b	Berke and Woodin, 2008
Majidae	<i>Naxia</i>	<i>tumida</i>	b	Berke and Woodin, 2008
Mithracidae	<i>Micippa</i>	<i>thalia</i>	a	Hultgren and Stachowicz, 2009
	<i>Microphrys</i>	<i>bicornutus</i>	b	Berke and Woodin, 2008
	<i>Thacanophrys</i>	<i>filholi</i>	a	Woods and Page, 1999
Pisidae	<i>Scyra</i>	<i>acutrifrons</i>	a	Hultgren and Stachowicz, 2009

#### 12.4.2.1 Body size and the evolution of crypsis vs. aposematic coloration

Hultgren and Stachowicz (2009) used phylogenetic comparative methods to test whether cost–benefit trade-offs mediated the evolution of decoration camouflage. They found a strong negative correlation between the extent of hooked setae (a morphological proxy for decoration camouflage) and adult body size among 37 different species of majoid crab. These interspecific decreases in decoration cover mirrored intraspecific decreases in decoration with ontogeny measured in that study, as well as numerous other studies (Table 12.3). Within species, increased reliance on camouflage in smaller individuals or juveniles mirrors patterns documented in many other animal species (Stoner *et al.*, 2003; Grant, 2007). Together these intra- and interspecific patterns suggest that decreases in decoration with body size may occur because larger individuals and species derive fewer benefits from decoration, relative to costs, than smaller species. Furthermore, comparative studies on aposematic prey suggests the converse: conspicuous coloration is associated with *increased* body size in dendrobatid frogs (Hagman and Forsman, 2003), and larger aposematic individuals or larger groups of aposematic individuals are easier to detect (Gamberale and Tullberg, 1996; Riipi *et al.*, 2001). Combined, these data suggest that size strongly influences the adaptive value of both aposematic and cryptic coloration or camouflage strategies.

#### 12.4.2.2 Evolution of alternative camouflage strategies

Although body size has pervasive effects on decoration extent throughout the majoid tree, multiple factors likely influence interspecific variation in decoration behaviour in the majoids. Across the majoid evolutionary tree, complete loss of decoration has occurred repeatedly (Hultgren and Stachowicz, 2008b, 2009) at several points in the majoid lineage. Many majoids that decorate little (or not at all) appear to rely on alternate camouflage strategies such as colour change. For one group of colour-changing majoids (genus *Pugettia*), phylogenetically controlled species comparisons demonstrate that the magnitude of colour change is negatively correlated with decoration extent, providing some evolutionary evidence for decoration–colour change camouflage trade-offs (Hultgren and Stachowicz, 2008a, 2009). Many non-decorating majoids in the



genus *Mithraculus* dwell in the interstices of coral rubble or form associations with structurally or chemically defended hosts (Table 12.4) (Patton, 1979; Wicksten, 1983; Coen, 1988; Gianbruno, 1989; Stachowicz and Hay, 1996, 1999a), and these habitat or host associations may serve as an alternate antipredator strategy minimising the need for decoration camouflage. Many majoid species living in deep-water habitats (*Rochina*, *Chorilla*, *Chionoecetes*) decorate minimally or not at all (Wicksten, 1993), and some species decorate less when found in deeper waters (Woods and McLay, 1994a), suggesting reduced predation in these habitats may select for decreased decoration. Comparative studies are a powerful tool with which to examine the influence of habitat or host associations on variation in camouflage behaviour (Ortolani, 1999; Stoner *et al.*, 2003; Caro, 2005), and further characterisation of the phylogenetic relationships and the habitat associations of majoids (and other lineages of camouflaged animals) could provide a greater understanding of the multiple factors influencing the evolution of camouflage behaviour in this group.

## 12.5 Future directions

The fascinating interplay of behaviour and morphology that characterises ‘decoration’ should continue to provide insights into the ecology and evolution of camouflage behaviour. Decoration has both a fixed aspect (hooks) and a flexible aspect (placement and choice of decoration) that helps make these organisms ideal targets for experimental studies of how flexible behaviours interact with morphology to determine camouflage function in a field setting. Furthermore, our growing understanding of phylogenetic relationships among species allows for increasingly rigorous comparative approaches to camouflage evolution. The potential for integration of behavioural, ecological, morphological, phylogenetic and developmental approaches is a real strength of using these crabs as model systems to address questions of camouflage evolution. We focus our suggestions for future inquiry on few of these integrative areas that we believe would prove particularly fruitful.

### 12.5.1 Origins of decoration

Wicksten (1993) offered the plausible hypothesis that decoration evolved from ‘food-gathering behaviour. This would certainly make the crab look less like a crab, and combined with other behaviours like restricted movements might rapidly be selected for to decrease susceptibility to predation. Evidence to date has not supported this hypothesis (Hultgren and Stachowicz, 2009), but additional insight would come from better understanding of the behavioural ecology and adaptive value of decoration in species that branch near the base of the majoid tree. For example, greater investigation of the reported food-catching behaviour of some Inachidae, or increased understanding of the phylogenetic distribution and functional morphology of different types of setae would help clarify the extent to which food caching might be an ancestral vs. derived function of decoration. Such approaches will require the integration of careful behavioural observations, functional morphology, and phylogenetics.

**Table 12.4** Examples of specialized host associations in the Majoidae

Majoid associate					
Family	Genus	Species	Reference	Location	Host relationship
Epiplatidae	<i>Huenia</i>	<i>heraldica</i>	Wicksten, 1983	Indo-West Pacific	Lives on and mimics coralline algae ( <i>Halimeda</i> spp.)
	<i>Huenia</i>	spp.	Griffin and Tranter, 1986	Indo-West Pacific	Lives on and mimics coralline algae ( <i>Halimeda</i> spp.)
	<i>Xenocarcinus</i>	<i>depressus</i>	Goh <i>et al.</i> , 1999	Singapore	Lives on and mimics coral ( <i>Melithaea</i> spp.)
	<i>Xenocarcinus</i>	<i>tuberculatus</i>	Tazioli <i>et al.</i> , 2007	Indonesia	Lives on and mimics coral ( <i>Cirripathes</i> spp.)
	<i>Inachus</i>	<i>phalangium</i>	Wirtz and Diesel, 1983; Rorandelli <i>et al.</i> , 2007a, b	Mediterranean	Associate of anemones ( <i>Anemonia sulcata</i> , <i>A. viridis</i> ); may not be obligatory
Inachidae	<i>Macropodia</i>	<i>linaresi</i>	Gianbruno, 1989	Italy	Associate of alcionarian corals (field observations)
	<i>Macropodia</i>	<i>rostrata</i>	Noted in Patton, 1979	Netherlands	Facultative associate of anemones ( <i>Anemonia sulcata</i> ) in some locations
Majidae	<i>Thersandrus</i>	<i>compressus</i>	Hay <i>et al.</i> , 1990	Caribbean	Associates with algae ( <i>Avrainvillea longicaulis</i> )
	<i>Mithrax</i>	<i>cinctimanus</i>	Patton, 1979	Jamaica	Associate of anemones ( <i>Stoichactis helianthus</i> and <i>Condylactis gigantea</i> )
Mithracidae	<i>Mithrax</i>	<i>forceps</i>	Stachowicz and Hay, 1999	North Carolina	Facultative associate with coral <i>Oculina arbuscula</i> , reduces epiphyte growth on coral
	<i>Mithrax</i>	<i>sculptus</i>	Coen, 1988	Belize	Facultative associate on the coral <i>Porites porites</i> ; decreases algal growth on corals
	<i>Mithrax</i>	<i>sculptus</i>	Stachowicz and Hay, 1996	North Carolina	Associates with coralline algae ( <i>Neogoniolithon strictum</i> ), reduces epiphyte growth on alga
Oregoniidae	<i>Hyas</i>	<i>araneus</i>	Noted in Patton, 1979	Scotland	Facultative associate of anemones ( <i>Tealia felina</i> ) in some locations
	<i>Hyas</i>	<i>coarctatus</i>	Noted in Patton, 1979	Netherlands	Facultative associate of anemones ( <i>Tealia felina</i> ) in some locations

### **12.5.2 Comparative approaches to understand variation in camouflage among species**

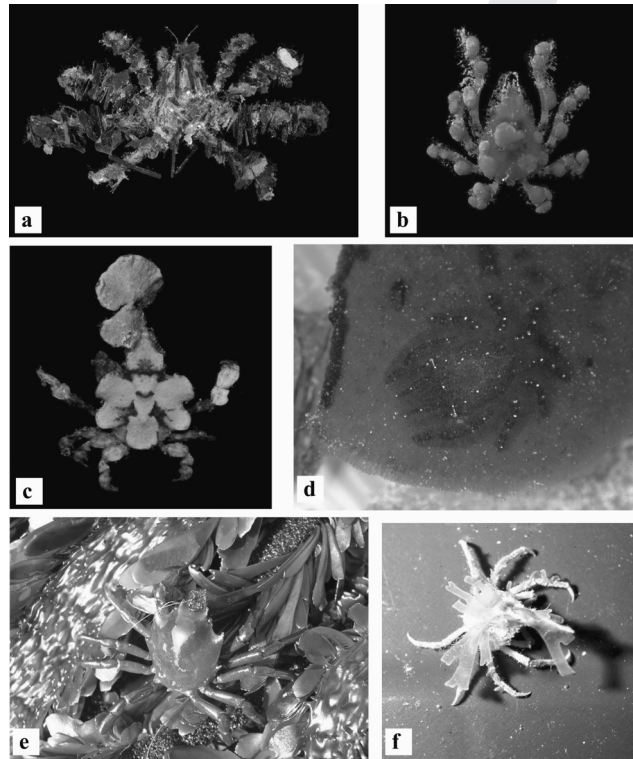
Another productive approach would be to further examine whether factors thought to drive intraspecific variation in decoration also operate across species (e.g., size; Hultgren and Stachowicz, 2009). For example, is the intraspecific increase in specialisation in lower latitudes exhibited by *Libinia dubia* also reflected in interspecific comparisons of temperate vs. tropical species? Intense predation pressure in the tropics is thought to drive the evolution of specialisation by many marine invertebrates, but because many of these animals use their hosts as both food and shelter, rigorously concluding that specialisation is driven by predator avoidance is difficult. Because choice of food and decoration can be decoupled in decorator crabs, the group holds promise for separating these two causes of specialisation. To date studies in this vein have only been conducted on single species (Stachowicz and Hay 1999b), but new phylogenetic data make it possible to do similar, phylogenetically controlled multi-species studies. Although specialist strategies occur across distantly related groups of majoids (Tables 12.1 and 12.4), most of these examples are scattered and we have little information on the decorating habits and phylogenetic relationships of majoids in tropical areas where predation intensity is greatest.

### **12.5.3 Synergistic effects of camouflage and other anti-predator behaviours**

Effective crypsis can involve not only the physical appearance of an animal, but behavioural traits that prevent detection (Stevens and Merilaita, 2009). The tractability of majoids as experimental organisms in the field and laboratory makes them an ideal group in which to study the role of behaviour in mediating the effectiveness of camouflage. For example, we know little about whether decorator crabs can select habitats to optimise camouflage, and how they recognise whether their camouflage or coloration matches the habitats. Experiments with colour-changing majoids suggest they use prior feeding experience, rather than visual cues, to select algal habitats with which they match (Hultgren and Stachowicz, 2010).

### **12.5.4 Links between development, behaviour and evolution**

Understanding the developmental pathways that lead to the expression of cryptic or aposematic coloration would provide additional insight into the evolution of these characters. In decorator crabs, for example, there appears to be little phylogenetic signal to the presence or absence of decoration behaviour, implying that it has been lost and perhaps regained several times. One striking pattern uncovered in the study of decorator crabs is the restriction of hooked setae (and thus decoration) to defined portions of the carapace and the appearance and loss of setae in these areas in discrete orders (Figure 12.4). This suggests that developmental processes might regulate expression of hooked setae on the carapace. A combination of developmental, genetic and morphological studies would be needed to assess this hypothesis, but it could lead to a better understanding of how decoration ability is gained and lost so many times throughout the majoid tree.



**Figure 12.6** Different forms of camouflage (decoration, mimicry and colour change) in decorator crabs. (a) A heavily decorated *Camposcia retusa* from French Polynesia; (b) a 'strawberry' spider crab (*Pelia mutica*) from Honduras, heavily decorated with sponges; (c) an epialtid spider crab (*Huenia* sp. cf. *heraldica*) from Moorea mimics the colour and morphology of its coralline algal host (*Halimeda* sp.; visible as decoration on right side of crab rostrum); (d) a majid crab *Thersandrus compressus*, well camouflaged against its chemically defended algal host (*Avrainvillea longicaulis*); (e) the Californian kelp crab *Pugettia producta* sequesters pigments from its algal habitat (*Egrecia menziesi*) in a form of colour change camouflage; (f) *Libinia dubia* decorates its carapace with chemically defended algae (*Dictyota menstrualis*). (Photographs: Arthur Anker (a, b, c); Jay Stachowicz (d, f); Kristin Hultgren (e).) See plate section for colour version.

## 12.6 Conclusions

Animal camouflage has long been used as a classic example of natural selection (Kettlewell, 1955), and many theoretical and experimental studies have explored the evolution of adaptive coloration (Merilaita and Lind, 2005; Berke *et al.*, 2006; Bond and Kamil, 2006; Cuthill *et al.*, 2006; Merilaita and Ruxton, 2007). However, few studies have examined the evolution of camouflage from an explicitly phylogenetic perspective (but see Ortolani, 1999; Stoner *et al.*, 2003). Decorator crabs have developed a stunning array of camouflage strategies – decoration, colour change and masquerade – to avoid predators in a wide range of habitats, and studies on this group can inform a greater understanding of the processes driving the evolution of camouflage in other animal

groups. Unlike many other animal groups with camouflage or coloration patterns that can be difficult to characterise, decoration camouflage in the majoids is strongly linked to a clear morphological trait – hooked setae – that is easily preserved and quantified in living and long-preserved specimens. As in many other animals, the effectiveness of camouflage in the majoids is dependent not only on physical appearance but by a suite of behavioural adaptations – habitat selection, decoration selection and adoption of sedentary behaviour – that further prevent detection or recognition. Finally, the wide variation in decoration behaviour both within and between majoid species makes it a model group in which to examine the factors influencing the evolution of camouflage – factors than may also influence camouflage in other groups.

## 12.7 Summary

Decorator crabs are most well known for their ‘decoration’ behaviour, a form of camouflage in which they attach materials from their environment to specialized hooked setae on their carapace. Because decoration is both morphologically constrained (i.e. by coverage of hooked setae), and behaviourally flexible (majoids must choose how much to decorate and what decoration materials to choose), it can be studied from a variety of different perspectives. Here we review camouflage in majoid crabs, and discuss how integrating studies of this group across different fields – ecology, behaviour and evolution – can contribute to our general understanding of the evolution and ecology of camouflage. We conclude that selection to avoid predation is a key factor driving variation in decoration camouflage, and that trade-offs between the energetic costs and anti-predator benefits of decoration may shape the evolution of camouflage in this group. Examining variation in decoration camouflage within species (in a geographic or ontogenetic context) and across species (in a phylogenetic context) has allowed these predictions to be tested evolutionarily, and suggest that the value of camouflage as a concealment strategy is strongly influenced by body size, both in decorator crabs and possibly in other groups of taxa relying on camouflage.

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