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Modelling the energy–mortality trade-offs of invertebrate decorating behaviour

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ABSTRACT

Background: Animals belonging to nearly 25% of the major metazoan phyla 'decorate' themselves with foreign material. Decoration occurs frequently in some taxa but infrequently in others. Some data indicate that decoration is a morphologically flexible phenotype that facilitates feeding and/or protects against biotic and abiotic forces. Yet decoration is not taxonomically ubiquitous. Other data suggest that decorating could be energetically costly.

Questions: How do feeding, energy expenditure, and mortality risk interact to exert selective pressure on decorating phenotypes? Could energetic costs associated with decorating theoretically limit the behaviour's selective advantage and account for its patchy taxonomic distribution?

Methods: Build a model of decoration's effect on reproductive potential using energy intake, energy expenditure, and mortality risk as parameters. Analytically find the upper bound of permissible energetic costs. From existing literature, estimate parameter values for energetics, reproduction, and mortality of the green sea urchin, *Strongylocentrotus droebachiensis*, and analyse them using graphical and numerical methods to determine the probable influence of energy cost on decoration in this animal.

Conclusions: Physiologically realistic energetic costs can constrain the parameter space in which decorating is selectively advantageous. This appears to be true even for costs far below the theoretical upper limit. Thus the evolution of decoration should be more sensitive to energetic costs than to the other parameters that we modelled. Sensitivity to energetic costs may explain (at least in part) decoration's patchy taxonomic distribution.

Keywords: camouflage, covering, defence, ornamentation, masking, predation, reproductive potential, selection.

INTRODUCTION

Throughout the animal kingdom, many organisms attach foreign materials to themselves or their structures. Examples include cnidarians, echinoderms, molluscs, polychaetes, arthropods, and vertebrates – nearly 25% of the major metazoan phyla (see

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http://www.evolutionary-ecology.com/data/2109Table.pdf). Such behaviours have variously been called covering, ornamenting, masking, hatting, carrying, shield-carrying, trash-carrying, or – as we prefer – decorating. 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.

Decoration occurs frequently within a handful of taxa, but infrequently elsewhere. It is particularly common within a few taxonomic clusters (see http://www.evolutionary-ecology.com/data/2109Table.pdf). For example, decorating insect larvae are common in four different orders, likely encompassing many tens to hundreds of species (see http://www.evolutionary-ecology.com/data/2109Table.pdf). Similarly, decorating is common in at least three families of brachyuran crustaceans, and for many genera of echinoids. Despite such 'nodes' of decorators, the phenotype is far from ubiquitous among animals in general. This patchy distribution suggests that the evolution of decorating phenotypes is somehow constrained. Circumstantial evidence implicates energetic costs as the constraining agents.

To determine whether energetic costs might realistically select against decorating phenotypes, we model the effect of decoration on reproductive potential using energy intake, energy expenditure, and mortality risk as parameters. Our model suggests that physiologically reasonable costs can constrain the parameter space in which decorating is selectively advantageous, potentially driving decoration's patchy taxonomic distribution. We summarize the literature on decorating across six phyla to establish that decorating (1) may decrease mortality risk, (2) may increase energy intake, (3) is morphologically unconstrained, and (4) may well be energetically costly. We then present the model and identify an analytic upper bound to permissible energy costs. Finally, we conduct graphical and numerical analysis using parameter values estimated from existing literature for a decorating sea urchin species. This analysis predicts that selection is, in fact, more sensitive to energetic costs than to other parameters. Even costs far below the theoretical upper bound are predicted to have a strong influence on reproductive potential.

BRIEF REVIEW OF DECORATING PHENOTYPES

Invertebrate decoration broadly serves two functions: protection and feeding [vertebrates may additionally use decoration as a mating signal (see review by Diamond, 1986)]. Protection can serve against predators or abiotic forces. Protection from predators can involve shielding, visual, tactile, or chemical crypsis, deterrence, and/or escape. Examples include some sea urchins [crypsis (Agatsuma, 2001); escape (Dayton *et al.*, 1970)], decorator crabs [crypsis (Wicksten, 1993; Amsler *et al.*, 1999; Stachowicz and Hay, 1999; Thanh *et al.*, 2003); deterrence (Stachowicz and Hay, 2000)], spiders [crypsis (Williams *et al.*, 2006)], caddisfly larvae [crypsis (Otto and Svensson, 1980; Johannson, 1991; Johansson and Johansson, 1992; Johansson and Nilsson, 1992)], assassin bug larvae [crypsis (Brandt and Mahsberg, 2002)], lacewing larvae [crypsis (Milbrath *et al.*, 1993; Lopez-Arroyo *et al.*, 1999; Eisner *et al.*, 2002)], and tortoise beetle larvae [shielding (Bacher and Luder, 2005); crypsis (Olmstead and Denno, 1992, 1993; but see Muller and Hilker, 1999)].

Decoration may cover vulnerable body surfaces, thereby protecting against ultraviolet (UV) radiation, sedimentation, thermal stress, or other physical forces. Examples include sea urchins [UV (Millott, 1956; Lees and Carter, 1972; Adams, 2001; Barnes and Crook, 2001; Verling *et al.*, 2002; Crook, 2003; Kehas *et al.*, 2005); sedimentation (Richner and Milinski, 2000)] and an anemone [desiccation

(Harte and Crowe, 1977; Richner and Milinski, 2000); UV (Dykens and Shick, 1984)]. Decoration might also increase stability or reduce spine breakage in flow for some sea urchins (Lees and Carter, 1972; James, 2000; Dumont *et al.*, in press). Decoration also reduces hydrodynamic scour on a polychaete's tube (B. Little and M. LaBarbera, unpublished data).

Many animals eat their decoration and/or small organisms living within it, as is the case for urchins (Pequignat, 1966; Ebert, 1968; Douglas, 1976), polychaetes (Mangum *et al.*, 1968; Woodin, 1977), and some crab species (Brenchley and Tidball, 1980; Mastro, 1981; Sanchez-Vargas and Hendrickx, 1987; Sato and Wada, 2000; Cruz-Rivera, 2001). Decoration can facilitate feeding by camouflaging the predator and therefore 'duping' prey, as demonstrated for assassin bug nymphs (Brandt and Mahsberg, 2002) and lacewing larvae (Milbrath *et al.*, 1993). Finally, decoration could allow organisms to forage safely as an alternative to seeking shelter, as is hypothesized for carrier snails (Kreipl and Alf, 1999) and urchins (Adams, 2001).

These examples demonstrate that decoration can be an advantageous phenotype that has common functions across taxonomic groups, and that it has evolved repeatedly in diverse morphological and ecological backgrounds. Why, then, is its taxonomic distribution so patchy?

One possibility is that decorating requires morphological pre-adaptations that only sometimes exist. We discount this, because decoration frequently occurs in taxa without specialized morphologies. Sea urchins carry material with their tube feet, which all echinoderms have. Polychaetes decorate with mucous secretions, which all tube-dwelling polychaetes make. Carrier snails use the same calcium carbonate secretions used to make shell. Morphological specialization does occur in some taxa, but does not appear to be a prerequisite. Thus, spider crabs and trash-carrying chrysopid larvae both have hooked setae that hold decoration (Wicksten, 1976, 1978, 1982; M.J. Tauber *et al.*, 1993; C.A. Tauber *et al.*, 2001), while dromiid, homoloid, and dorippid crabs use modified walking legs, and tortoise beetle larvae use exoskeletal spines (Muller and Hilker, 1999). However, arthropods exhibit tremendous diversity in the form and function of appendages and exoskeletal outgrowths (see, for example, Panganiban *et al.*, 1997), so the evolution of specialized setae or spines is unlikely to be limiting – as, in fact, is evidenced by the huge number of decorating arthropods (see http://www.evolutionary-ecology.com/data/2109Table.pdf). Thus, although morphological pre-adaptation sometimes occurs, it cannot be considered a prerequisite for decorating.

A more likely limiting factor is energetic cost. Clearly, energy must be expended to add and carry decoration, as several authors have intuited (Wicksten, 1983; Richner and Milinski, 2000; Kehas *et al.*, 2005; Dumont *et al.*, in press). Obviously, one would infer that the benefits of decoration overwhelm any costs for those species that decorate. Nonetheless, the ontogenetic and taxonomic patterns of decorating suggest that costs play a significant role in shaping the phenotype's evolution. For example, many animals that decorate as juveniles reduce or stop decorating as adults, including several crab species (Wicksten, 1979; Mastro, 1981; Stachowicz and Hay, 1999), some urchins (Dumont *et al.*, in press), gastropods (Linsley & Yochelson, 1973; Crook, 2003), and all decorating insects (see references at http://www.evolutionary-ecology.com/data/2109Table.pdf). Such ontogenetic shifts would be expected if costs – energetic or otherwise – select against decorating when animals achieve a size refuge from predation or other threats. Some studies have quantified costs associated with decorating for crustaceans (Herreid and Full, 1986; Berke and Woodin, 2004), although the jury is still out for the few insects studied (Olmstead and Denno, 1992; Bacher and Luder, 2005). If energetic costs are real, could they be significant enough to limit the evolution of decorating?

MODEL

We choose fitness as the common currency for energy and mortality, a concept pioneered in state variable models (McNamara and Houston, 1986). Specifically, we model fitness using 'reproductive potential', a term that we adapt from Fisher's (1930) reproductive value. Individual reproductive value is typically given as the product of an individual's expected fecundity (Fisher's b_x term) and survivorship (Fisher's l_x/e^{mx} term), usually integrated over multiple age classes (Fisher, 1930; McNamara and Houston, 1986; Mangel and Clark, 1988; Caswell, 1989; Case, 2000) [for a related discussion of modelling fitness with life-history data, see McGraw and Caswell (1996)]. Drawing on this, we focus on a single age class, expressing reproductive potential as a function of the amount of decoration d [unlike Wicksten's (1993) model for crab decorating, which treated decoration as the dependent variable]. We begin with some assumptions:

i. The decorating phenotype can invade if adding a single piece of decoration increases an organism's fitness.
ii. Selection is negative for very large amounts of decoration.
iii. The amount of decoration varies within a population, corresponding to variations in fitness.
iv. There is only one age class.
v. Reproductive potential is evaluated as an accumulation over a fixed time interval (e.g. a single day or season).
vi. Fecundity is directly linked to energy intake.

Mortality components

The mortality term has two components, biotic and abiotic, both expressed as probabilities. Biotic mortality, $P(d)$, includes predation, disease, and competition; however, decoration is primarily expected to influence predation. All parameters in all expressions that follow are assumed to be positive except where indicated. Predation risk $P(d)$ declines exponentially as decoration is added. Decoration might carry units of mass, volume or surface area, as appropriate for different organisms; we will simply use generic units.

$$P(d) = P_0 \exp(-pd) \tag{1a}$$

where P_0 = likelihood of biotic mortality (predation), p = decay rate due to decoration (d^{-1}), and $P(d)$ and $P_0 \leq 1$.

Abiotic death risk $N(d)$ describes how decoration affects risk from environmental hazards such as wave surge, ultraviolet radiation, and desiccation. $N(d)$ is quadratic, reflecting our assumption (ii), that very large amounts of decoration should theoretically increase mortality risk (e.g. by crushing).

$$N(d) = \min\{N_0 - n_1 d + n_2 d^2, 1\} \tag{1b}$$

where N_0 = likelihood of abiotic mortality, n_1, n_2 = constants (d^{-1} and d^{-2}), and $N(d)$ and $N_0 \leq 1$.

Combining risks of predation and abiotic death gives net mortality risk (Fig. 1A), the form of which precludes death by multiple causes:

$$M(d) = 1 - [(1 - P(d))(1 - N(d))] \tag{1c}$$

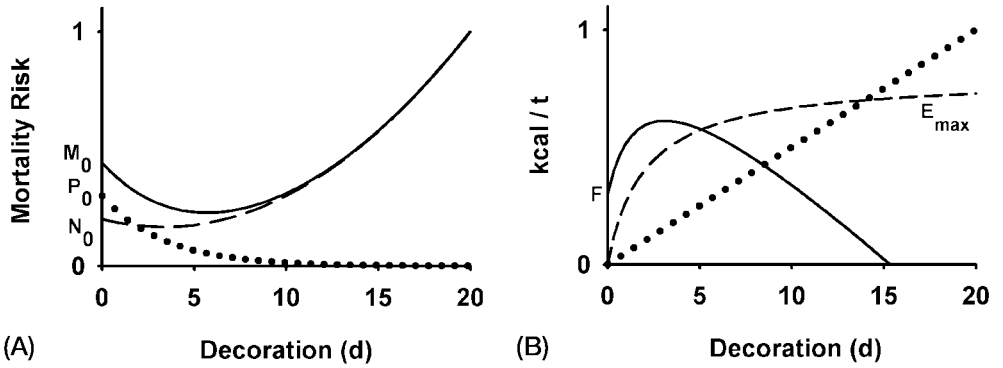

Fig. 1. Curves showing the predicted effects on mortality risk (A) and energy intake (B) as decoration is added. (A) Mortality is a composite of predation and abiotic sources (e.g. desiccation). As decoration is added, predation risk decreases exponentially (dot). Risk of death from abiotic sources first decreases but then increases as excessive decoration inhibits movement, exerts crushing force, and so on (dash). Net mortality is determined by equation (1c) (solid). (B) Net energy intake is a composite of energetic costs and benefits. As decoration is added, it confers energy benefits that allow the organism's caloric intake to increase to E_{max}, a physiological upper limit (dash). Decoration also incurs the energetic cost of adding and carrying decoration (dot). When costs are subtracted from benefits, net energy intake increases to some maximum, after which costs begin to overwhelm benefits (note that a basal feeding rate F is included) (solid).

Energy components

Energy intake is separated into energetic costs and benefits. The energetic benefit $E(d)$ is the increase in energy intake due to decoration, which we model as a Holling type II functional response. All energy functions carry units of energy intake (e.g. kilocalories) during the fixed time period.

$$E(d) = (E_{max}d)/(k + d) \tag{2a}$$

where E_{max} = maximum intake and $k = d$, where $E(d) = E_{max}/2$.

The energetic cost function $C(d)$ should be strictly increasing, but might be linear, exponential, logistic, or something else. To minimize assumptions, we choose a linear function:

$$C(d) = cd \tag{2b}$$

where c = cost coefficient (kcal $\cdot$ d^{-1}). Note that variants requiring more assumptions – such as mixing initial near-linear growth with eventual skyrocketing cost, $C(d) = c_1 d/(c_2 - d)$ – behave identically to equation (2b) for d close to 0, which will be a principal region of interest.

A net energy function $\varepsilon(d)$ (Fig. 1B) is given by

$$\varepsilon(d) = F + E(d) - C(d) \tag{2c}$$

where F = basal feeding rate (kilocalories over time period).

Reproductive potential

Invoking our assumption that fecundity is linked directly to energy intake, we designate a linear conversion factor a, representing an organism-appropriate measure of fecundity per kilocalorie for a fixed time interval [recall that a similar conversion term appears in the classical Lotka-Volterra equations (Volterra, 1926)]. Fecundity is often related to energy intake (Larson *et al.*, 1980; Wallin *et al.*, 1992; Carli *et al.*, 1995; Minor and Scheibling, 1997; Middleton and Gurney, 1998; Russell, 1998; Djunaidah *et al.*, 2003). Although the relationship is most likely non-linear, there is no evidence that decoration has a direct influence on fecundity (at least for invertebrates), so even if a were non-linear it would effectively be a constant in the context of this model. We propose, then, the following reproductive potential equation:

$$R(d) = a\varepsilon(d)[1 - M(d)] \tag{3}$$

Here, the $a\varepsilon(d)$ term represents fecundity and the $1 - M(d)$ term represents survivorship, where $\varepsilon(d)$ and $M(d)$ are given by equations (2c) and (1c) respectively. All reproduction is implicitly assumed to occur at the end of the interval.

MODEL ANALYSIS

An invasibility criterion for decorating is $R'(0) > 0$, reflecting assumption (i), that adding a single piece increases reproductive potential. We analytically identify the upper bound on energetic costs by determining a necessary condition on c, solving for c such that $R'(0) > 0$:

$$c < F(n_1/(1 - N_0) + pP_0/(1 - P_0)) + E_{\max}/k \tag{4}$$

This inequality simply shows that greater benefits render higher costs permissible. We will see that $R(d)$ is actually more sensitive to the parameter c than to other model parameters, a result that one would not predict from first principles. Furthermore, sensitivity to c is high even at values far below the upper limit.

The critical point d^*, where $R'(d) = 0$, and the value $R(d^*)$ together convey significant information regarding the parameter space within which decoration is selectively advantageous. Because $R'(0) = 0$ has no simple analytic solution, we will use numerical and graphical methods of sensitivity analysis.

Parameter estimation

Numerical analysis requires parameter values, some of which can be extrapolated from existing data. When there are no data, we assign values for the sake of model testing, using qualitative knowledge as much as possible. The primary purpose of these estimates is to facilitate analysis; they also allow us to crudely assess the biological accuracy of the model, but to fully test the model will require extensive experimentation.

Given the extensive literature base for the green urchin *Strongylocentrotus droebachiensis*, we will use it as a test system. Green sea urchins are known to decorate as protection against UV radiation (Cheung and Lam, 1999; Adams, 2001). Other urchin species enjoy protection from wave surge, sedimentation, and predation as a function of decoration (Lees and Carter, 1972; Amsler *et al.*, 1999; Richner and Milinski, 2000; Agatsuma, 2001; Barnes and Crook, 2001), and may also eat their decoration (Ebert, 1968; Dix, 1970; Amsler *et al.*, 1999; personal observation). Existing energetic and mortality data for *S. droebachiensis* are sufficient to estimate parameter values for the purposes of

sensitivity analysis. Unfortunately, these studies do not report the degree or persistence of decoration. *Strongylocentrotus droebachiensis* exhibits quite variable decorating behaviour, making it unlikely that all of the urchins were decorated at any given time or that any single urchin decorated throughout any experiment (personal observation). Despite the preliminary nature of our estimates, this exploration nonetheless generates interesting predictions which should be robust to changing parameter values.

Energy parameters are estimated from *S. droebachiensis* feeding data. The feeding rates F and $E_{\mathbf{max}}$ should theoretically represent energy absorbed, adjusted for baseline metabolic requirements. Because food consumption data are more often reported, we base our estimates on food intake (using absorption would change our estimates by 20–60%, but since all energy parameters would change this would not have a qualitative effect on the model). Many studies report feeding rates (Vadas, 1977; Larson *et al.*, 1980; Thompson, 1983; Lemire and Himmelman, 1996; Minor and Scheibling, 1997; Russell, 1998; James, 2000; Vadas *et al.*, 2000), but we focus on Larson *et al.* (1980), who give caloric intake and the ensuing gonad mass for several diet treatments [Vadas (1977) gives similar data for a single diet treatment, which generally agrees with the work of Larson *et al.*]. Green urchins consumed roughly 0.3 kcal $\cdot$ day^{-1}, averaged across diets and seasons (Larson *et al.*, 1980). Thus, we assign 0.3 kcal as the basal feeding rate F, taking the fixed time interval to be one day. Maximum consumption, during the summer with a favourite algae given *ad libitum*, was roughly 0.8 kcal $\cdot$ day^{-1}, which we take as the maximum feeding rate $E_{\mathbf{max}}$. The half-saturation point of the energy intake curve, k, cannot be estimated from the literature, so we will arbitrarily set $k = 2$ g (sensitivity analysis shows that changing k has little effect on the model's behaviour). The energetic cost per unit of decoration, c, can be crudely estimated as follows: Urchins eat at least 4% of their body mass each day (Larson *et al.*, 1980). If we assume that carrying 1 g of decoration is calorically equivalent to maintaining 1 g of body mass, then each gram of decoration might cause the animal to eat an extra 0.04 g of food per day. The average caloric value of food items was 0.67 kcal $\cdot$ g^{-1} [summer average, all diets (Larson *et al.*, 1980)], prompting the estimate of (0.04 g $\cdot$ day^{-1}) $\times$ (0.67 kcal $\cdot$ g^{-1}) $\approx$ 0.03 kcal $\cdot$ day^{-1} for each gram of decoration, our estimate for c (Table 1).

Energy-to-offspring conversion

Several studies report that caloric intake influences gonad mass for urchins (Thompson, 1983; Lemire and Himmelman, 1996; Minor and Scheibling, 1997; Russell, 1998; Vadas *et al.*, 2000). Again, we follow Larson *et al.* (1980) because they report end-of-year gonad mass for different diet treatments. Using Larson *et al.*, we plot end-of-year gonad mass versus caloric intake for each of several diet treatments (not shown). Fitting a line yields a slope of 13.3 g (gonad $\cdot$ year^{-1})/(kcal $\cdot$ day^{-1}) ($R^2 = 0.77$) [gonad mass consistent with Minor and Scheibling (1997)]. This can be converted to 0.04 g gonad $\cdot$ kcal^{-1}, our estimate for a (Table 1).

Mortality parameters

Strongylocentrotus droebachiensis in the Northwestern Atlantic experience 12–16% annual mortality in the field (Russell *et al.*, 1998) (this is consistent with Ebert *et al.* (1999) and Chen and Hunter (2003) for related *Strongylocentrotus* spp.). Most studies do not differentiate among causes of death. However, when queried, Russell agreed with our intuition that predation accounts for more deaths than other causes in that habitat (M.P. Russell, personal communication). Disease can be an important factor in urchin mortality in other habitats, and disease death rates are included in P_0. Using this qualitative knowledge, we divide the 0.12 basal mortality

Table 1. Estimated parameter values

Model component	Parameter	Definition	Value	Source
Mortality risk	P_0	Basal predation risk	0.08	Average mortality on *S. droebachiensis* is 0.12 (Russell *et al.*, 1998). We assume that most mortality is predation
Mortality risk	p	Decay rate for predation curve	0.347 (d^{-1})	Given $P_0 = 0.08$, $p = 0.347$ generates a curve with a minimum at $d = 6$, chosen arbitrarily
Mortality risk	N_0	Basal risk of abiotic death	0.04	By the same logic used for P_0 (Russell, 1998)
Mortality risk	n_1	Linear coefficient in abiotic death function	0.02 (d^{-1})	By logic similar to p estimation, see text
Mortality risk	n_2	Quadratic coefficient in abiotic death function	0.0026 (d^{-2})	By logic similar to p estimation, see text
Energy	F	Basal feeding rate	0.3 (kcal)	Average feeding rate (Larson *et al.*, 1980)
Energy	E_{max}	Maximum rate of energy intake	0.8 (kcal)	Maximum feeding rate (preferred diet during the summer; Larson *et al.*, 1980)
Energy	k	Half-saturation constant of energy benefit curve	2 (d)	Arbitrary
Energy	c	Cost per unit decoration for the linear cost model	0.03 (kcal·d^{-1})	From data on feeding rates and body mass (Larson *et al.*, 1980); see text
Reproductive potential	a	Energy-offspring conversion	0.04 (fecundity per kcal)	From data on gonad mass and diet (Larson *et al.*, 1980); see text

Note: Values were extrapolated from literature for the green sea urchin *Strongylocentrotus droebachiensis* when possible (see text). Units given in parentheses; rates not given in units of time because we assume a single time period.

rate into basal predation (P_0) and abiotic death (N_0) rates, arbitrarily setting the probability of predation as twice that of other mortality sources, giving $P_0 = 0.08$ and $N_0 = 0.04$ (Table 1). We then speculate on the predation decay rate p by assuming that $P(d)$ approaches 0 when d is large (say $d > 6$ g, chosen arbitrarily). Solving for p gives $p = 0.347$ (Table 1).

Having already set $N_0 = 0.04$, we assign the parameters n_1 and n_2 by invoking our assumption that abiotic death is certain for very large amounts of decoration, in the vicinity of $d = 20$. We then suppose that a minimum occurs at intermediate d-values. Iteratively testing values shows that if $n_1 = 0.02$ and $n_2 = 0.0026$, a minimum occurs at (3.8, 0.002) and $N(d) = 1$ for $d \geq 23$, an admittedly arbitrary curve that reflects our intuition and provides a starting point for model testing.

Graphical analysis

Because there is no simple analytic solution for $R'(0) = 0$, we will employ graphical and numeric methods to analyse the model using parameter estimates in Table 1 as starting points. Even with crude parameter estimates, $R(d)$ behaves as predicted (Fig. 2A). The invasibility criterion is satisfied ($R'(0) > 0$), and the curve spans decoration masses from 0 to 40 g, a reasonable range for urchins of 50–100 g (personal observations).

Until now we have assumed that energy and mortality benefits both occur. What happens when only one benefit occurs, as is apparently the case for most insects and possibly other decorators? (see http://www.evolutionary-ecology.com/data/2109Table.pdf). If only energy benefits occur, the $R(d)$ curve is positive over a greater range of d, but peaks at one-tenth the reproductive potential ($R(d^*) = 0.0034$ vs. 0.03; Fig. 2B). This suggests that, all things being equal, a species obtaining only energy benefits might experience weaker selection as well as greater variance than species obtaining compound benefits. When only mortality benefits occur, $R(d)$ decreases monotonically (Fig. 2C), indicating that energy costs overwhelm mortality benefits for this set of parameters.

Sensitivity analysis

Selective pressures might well vary over space and time, reflecting changing physiological states, predator densities, abiotic conditions, and so on. We apply numerical sensitivity analysis to ask how varying parameters might affect reproductive potential. To do this, we trace the critical value d^* over a range of parameter values. Because d^* is the theoretically 'optimal' amount of decoration, it can be used as an indicator for selective pressure. We also examine the qualitative behaviour of the $R(d)$ curve over a range of parameter values, looking particularly at (1) the range of d for which $R(d) > 0$ and (2) the maximum value itself, $R(d^*)$. The range in which $R(d)$ is positive is the beneficial range of decoration for which fitness is greater than that of an undecorated organism. We infer that the value $R(d^*)$ qualitatively reflects the strength of selection, since higher reproductive potential would presumably constitute stronger selective pressure to decorate.

Of the energy parameters, reproductive potential is most sensitive to the energetic cost parameter c. Figure 3 shows that slightly increasing costs might exert strong selective pressure for smaller amounts of decoration (smaller d^*). Such sensitivity is surprising because our estimate for c (0.03 kcal$\cdot$g^{-1}) is far below the theoretical upper limit of c, which in this case is 0.5 kcal$\cdot$g^{-1} (obtained by substituting values from Table 1 into inequality 4a). This suggests that energetic costs could play an important role in selection, even when they are small compared with energy intake. Sensitivity to c is mitigated when $E_{\max}$ is large (Fig. 3); nonetheless, reproductive potential is relatively insensitive to the half-saturation constant k (especially when $k > 1$), and is only moderately sensitive to the feeding rates $E_{\max}$ and F (F not shown) – although sensitivity to these increases when c is high (not shown). Thus, selection is expected to be affected both directly and indirectly by the energetic costs per unit of decoration.

Of the mortality parameters, reproductive potential is most sensitive to n_1 and n_2, which govern the shape of the abiotic mortality function $N(d)$ (Fig. 4). Increasing n_1 (which is mutually dependent on n_2) reflects very strong benefits, as $N(d)$ decreases more rapidly. Predation benefits can strongly affect $R(d)$, but only when predation risk is high (see Fig. 5). Surprisingly, $R(d)$ is relatively insensitive to predation decay rate p, except at very small

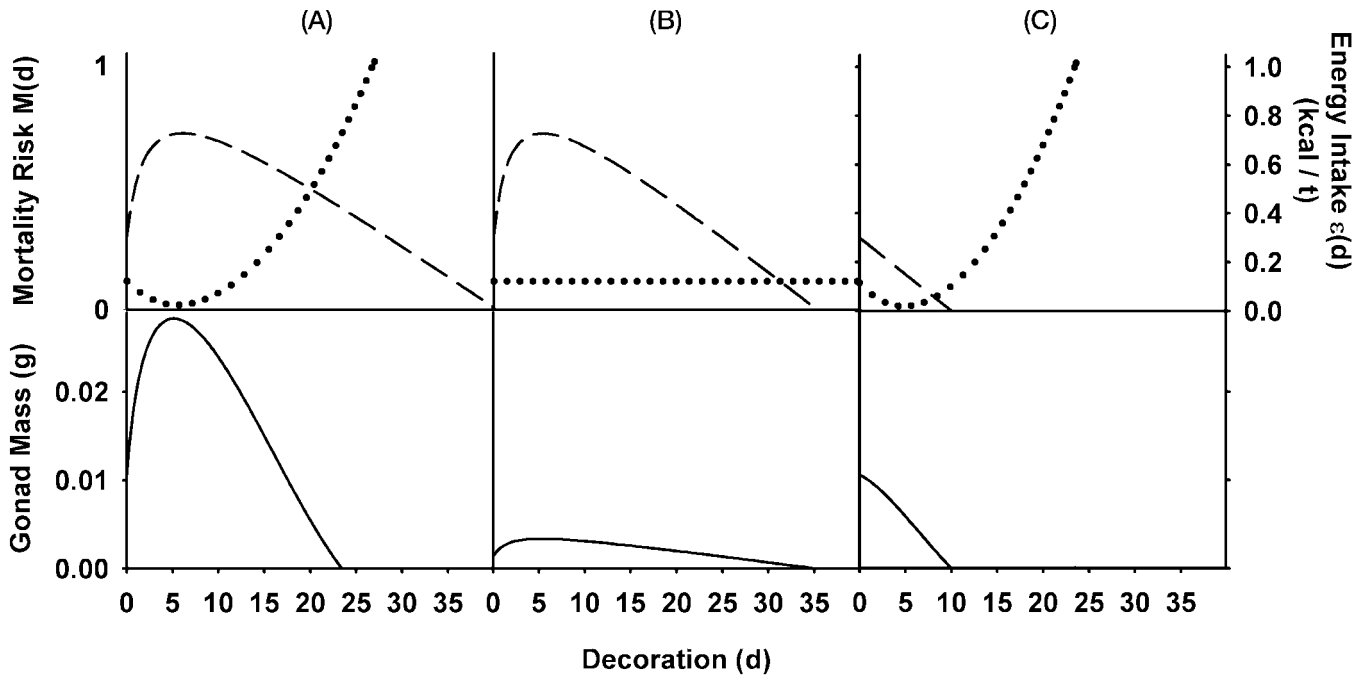

Fig. 2. Predicted reproductive potential – measured by gonad mass – as decoration is added, assuming different combinations of energy and mortality benefits, all other parameters being fixed (Table 1). $R(d)$ is measured here by gonad mass per day. (Top) The energy (dash) and mortality (dot) curves for each scenario. (Bottom) The resulting reproductive potential curves (solid). (A) When both energy and mortality benefits exist, reproductive potential is expected to increase to some maximum beyond which costs are overwhelming. Note that, in spite of rough parameter estimates, the reproductive potential curve initially increases, as expected. d^* is the d-value of the critical point in $R(d)$, used for sensitivity analysis. *Strongylocentrotus droebachiensis* is believed to experience energy and mortality benefits, making this a likely scenario. (B) When only energy benefits exist, mortality is unaffected by decoration and so becomes a constant. The $R(d)$ curve is damped, but positive for a large range of d. (C) If only mortality benefits exist, the energy cost remains. For the parameters in Table 1, costs overwhelm mortality benefits, causing the $R(d)$ curve to initially decrease, indicating selective disadvantage. One would not expect systems having negative $R(d)$ curves to decorate. Different parameter values, with lower costs relative to benefits, can result in an $R(d)$ curve that increases initially.

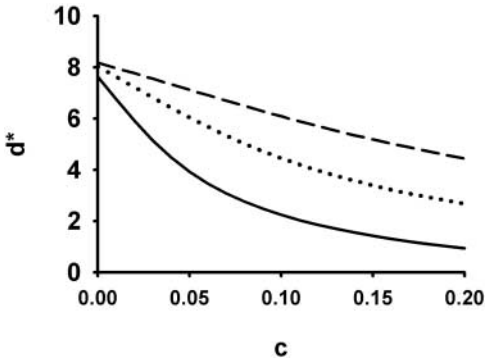

Fig. 3. Sensitivity to the unit energy cost c. As the maximum energy benefit E_{max} increases, the curve d^* vs. c becomes shallower, indicating reduced sensitivity to c. $E_{max} = 0.8$ (solid), 2.0 (dot), 4.0 (dash). By the same token, increasing c reduces sensitivity to E_{max}. All parameters except c and E_{max} have values as in Table 1.

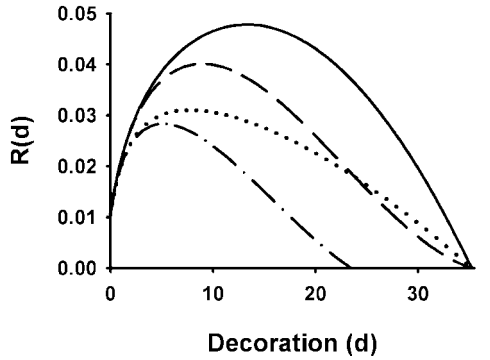

Fig. 4. $R(d)$ curves for different n_1 and n_2 values. Increasing n_1 or decreasing n_2 has three effects: the $R(d)$ curve becomes positive for a greater range of d, d^* shifts to the right, and $R(d^*)$ increases. $n_1 = 0.08$ (solid and dash) or 0.02 (dot and dash-dot); $n_2 = 0.0001$ (solid and dot) or 0.0026 (dash and dash-dot). All other parameters have values as in Table 1.

values (Fig. 6). Sensitivity to p is greatest when basal predation risk P_0 is large ($P_0 > 0.3$; Fig. 5; unlike n_1 which influences $R(d)$ even when N_0 is low) or when p is small, both of which slow the decrease in $P(d)$, giving it a larger role in the overall mortality function. For Table 1 parameter values, $R(d)$ is insensitive to the predation decay rate p because P_0 is relatively small (not shown). This is consistent with data suggesting that urchin decorating in general, and especially in *S. droebachiensis*, may have little to do with predation risk (Barnes and Crook, 2001; Dumont *et al.*, in press; but see Amsler *et al.*, 1999; Agatsuma, 2001).

How do energy and mortality parameters interact? Changing c at the same time as n_1 or p can have a qualitatively different effect on $R(d)$ than changing either parameter alone. In changing p and c together, p dominates the value $R(d^*)$ while c dominates the range $R(d) > 0$ (Figs. 6 and 7). In changing n_1 and c together, c dominates in constraining both the range $R(d) > 0$ and the value $R(d^*)$ (Fig. 8). This is true even if c increases very slightly and n_1 increases by an order of magnitude (not shown). Furthermore, when c is large and held

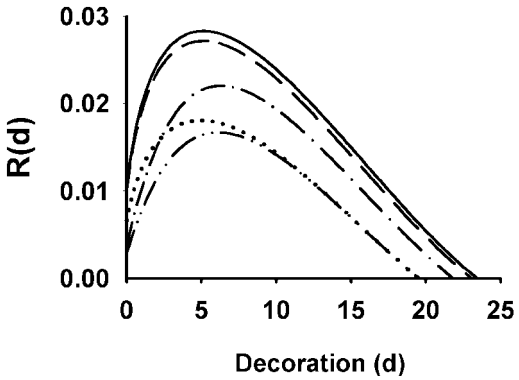

Fig. 5. $R(d)$ curves for different N_0 and P_0 combinations: $P_0 = 0.08$ (solid, dash, and dot) or 0.6 (dash-dot and dash-dot-dot); $N_0 = 0.04$ (solid), 0.08 (dash), 0.2 (dash-dot) or 0.4 (dash-dot and dash-dot-dot). When P_0 is small, a two-fold increase in N_0 has little effect; when P_0 is large, a two-fold change has a much greater effect. An order of magnitude change in N shrinks $R(d^*)$ and the range where $R(d) > 0$, without affecting d^*. An order of magnitude change in P_0 decreases $R(d^*)$ and shifts d^* to the right.

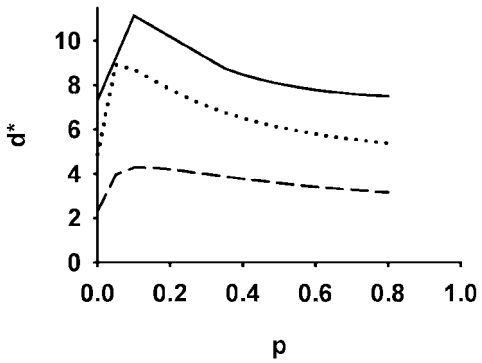

Fig. 6. Sensitivity to predation decay p for different values of the rate of change c of energy cost: $c = 0.001$ (solid), 0.03 (dot) or 0.09 (dash). All values except p, c, and P_0 have values as in Table 1; $P_0 = 0.8$ to show sensitivity to p (if P_0 were small, as in Table 1, the model would be insensitive to p; see text). Changing the rate at which energetic costs increase qualitatively and quantitatively changes sensitivity to p; as the cost rate increases, the magnitude of change in d^* diminishes and the curve flattens out.

constant, increasing n_1 changes only the height of $R(d)$, not its range, suggesting that the sensitivity to n_1 is constrained by c (Fig. 8).

These patterns suggest that energy costs dominate the strength of selection (because $R(d^*)$ changes) as well as the advantageous range of decoration (because the range of d changes), which should be reflected in population-level variance patterns. Furthermore, interactions between parameters might well lead to an irregular parameter space in which small variations, particularly in energetic costs, can limit the phenotype's selective advantage. The value d^* is most likely sensitive to the combined effect of all parameters, and

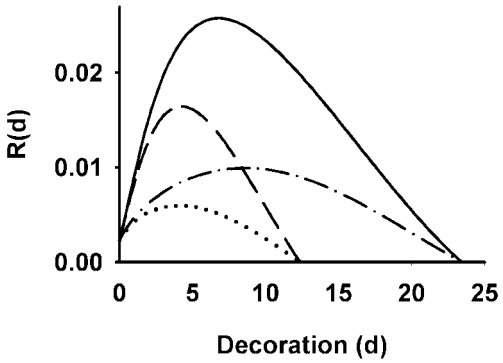

Fig. 7. $R(d)$ curves for different p and c combinations: $p = 0.347$ (solid and dash) or 0.03 (dash-dot and dot); $c = 0.03$ (solid and dash-dot) or 0.08 (dash and dot) Increasing predation decay rate p increases the value of $R(d^*)$, but not the beneficial range of d. Decreasing energy cost rate c increases $R(d^*)$ as well, but also extends the beneficial range. All values except p and c have values as in Table 1.

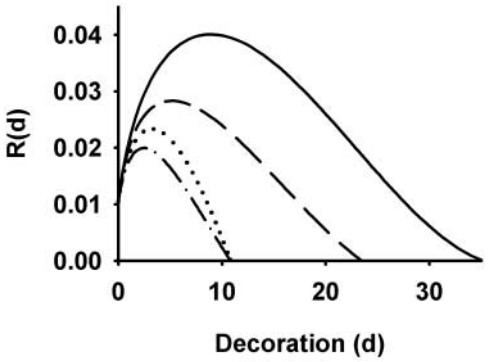

Fig. 8. $R(d)$ curves for different n_1 and c combinations: $n_1 = 0.08$ (solid and dot) or 0.02 (dash and dash-dot); $c = 0.03$ (solid and dash) or 0.09 (dot and dash-dot). When c is large, increasing n_1 changes only $R(d^*)$. However, when c is small, increasing n_1 changes $R(d^*)$ as well as the range of d where $R(d) > 0$. Decreasing c makes the effects of changing n_1 qualitatively different. All values except n_1 and c have values as in Table 1.

hence 'optimality' may seldom be observed. This potentially important role of energetic costs has been experimentally neglected.

CONCLUSION

Predation risk, physical stresses, and feeding pressures appear to maintain decorating phenotypes in morphologically and ecologically diverse lineages (see http://www.evolutionary-ecology.com/data/2109Table.pdf). These advantages are probably tempered by the costs of decorating. Our model suggests that selection is sensitive to energetic costs, even when such costs are far below the theoretical upper limit. Significantly, this suggests that even modest costs might constrain the parameter space in which decoration is advantageous (Figs. 2, 6, and 7).

The costliness of decorating has been experimentally supported for some arthropods [hermit crabs (Herreid and Full, 1986; Amsler *et al.*, 1999); spider crabs (Berke and Woodin, 2004); see also Otto (2000)]. Contrasting data exist for some cassidine larvae (Olmstead and Denno, 1992; Bacher and Luder, 2005), some of which might avoid costs by being slow-moving (Olmstead and Denno, 1992). Indeed, many decorators are sessile or slow-moving. Being inactive undoubtedly improves crypsis (Robinson, 1969; Wicksten, 1983), but might also reflect the difficulty of being active while decorating. Using more active cassidines, Bacher and Luder (2005) found that decoration had no effect on pupation-associated weight change for larvae fed *ad libitum*, a valid approach that nonetheless might not reveal modest costs. Berke and Woodin (2004) measured weight loss during starvation in spider crabs and found that decoration causes increased weight loss. This approach does not reflect field conditions, but has the advantage of rendering costs more detectable.

These difficulties aside, the widespread occurrence of ontogenetic shifts in decorating suggests that costs of some sort have selectively favoured larger individuals that decorate less. Future research should assess the magnitude and frequency of energetic costs among decorating species. The most appropriate method might be system-specific, but measuring metabolic rate, growth or activity level should be informative and feasible for most organisms. Experimental studies of the function of decoration are also required. Decoration's multiple effects on the organism, together with its taxonomic prevalence and empirical manipulability, make it an interesting system for studying the evolution of complex behavioural phenotypes.

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