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Fragments or propagules? Reproductive tradeoffs among *Callyspongia* spp. from Florida coral reefs

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Fragmentation and propagule formation are alternative reproductive strategies found in both plants and animals, with the latter generally providing greater dispersal capability. When both strategies occur, life history theory predicts that resources should be divided between the two. On coral reefs, both strategies are exhibited by branching corals and sponges, which are broken-up after storm events and rapidly recolonize. In this study, we compared two congeneric Caribbean reef sponges, *Callyspongia armigera*, which is branched and easily fragmented, and *C. vaginalis*, which is not, to test whether there is a tradeoff in growth and propagule formation for *C. armigera* relative to *C. vaginalis*. Both species were equally abundant on coral reefs off Key Largo, Florida (10.1 ± 3.7 vs 11.9 ± 3.0 per 100 m^2, respectively), suggesting that they are equally successful relative to two other non-fragmenting congeneric species (*C. fallax* and *C. plicifera*) that are much less common. The number of substratum attachment points per sponge was significantly higher for *C. armigera* compared to *C. vaginalis* (2.31 ± 1.47 vs 1.03 ± 0.18 $sponge^{-1}$), providing further evidence of the reliance of *C. armigera* on fragmentation, and of *C. vaginalis* on recruitment from larval settlement and subsequent growth. Growth rates in predator-exclusion experiments were ~4-fold higher for *C. armigera* compared to *C. vaginalis* (0.36 ± 0.31 vs 0.08 ± 0.11 % initial mass day^{-1}), but *C. armigera* produced ~13-fold fewer propagules than *C. vaginalis* (0.04 ± 0.22 vs 0.53 ± 1.08 % tissue area). Our results support a tradeoff between growth and propagule output for *C. armigera* relative to *C. vaginalis,* suggesting that these closely related sponge species took different evolutionary trajectories in reconciling their resource constraints.

Resource tradeoffs are implicated when two contrasting life history strategies co-exist (Stearns 1992). For example, plants may primarily reproduce through propagule formation (e.g. seeds) or by asexual fragmentation (e.g. rhizomes, runners, plantlets). Plants allocate resources to physiological functions such as growth and reproduction from a finite pool (Coley et al. 1985, Bazzaz et al. 1987). A tradeoff arises when plants allocate resources to vegetative growth for fragmentation instead of propagule formation, just as there are tradeoffs between reproductive and somatic investments in animals (Cody 1966).

Propagule formation as a reproductive strategy provides several advantages. Propagules are smaller and lighter than fragments and are able to disperse further (Gaylord et al. 2002). Also, most propagules are sexual, which confers the advantages that sexual recombination provides, enabling selection to break down negative gene combinations at different genetic loci and increase genetic diversity (Hoekstra 2005, Charlesworth 2007). In addition to providing short-term advantages in rapidly fluctuating or biologically complex environments where new selective forces constantly occur, sexual reproduction also decreases competition between siblings by increasing diversity among them (Williams 1975, Maynard Smith 1978).

Yet, fragmentation also provides benefits. By investing in vegetative growth, plants can increase in biomass that is directly used to colonize new areas (Abrahamson 1975). Fragmentation of plants may reduce the spread of infection between clones (Hay and Kelly 2008). For aquatic plants, fragments can be carried by flowing water to colonize new locations. In one example, reproductive strategies and dispersal outcomes were very different for two groups of riverine plants used in disturbance experiments: fragments of *Sparganium emersum* and *Ranunculus trichophyllus* rooted and re-established themselves quickly, whereas *Luronium natans*, *Hippuris vulgaris* and *Elodea canadensis* produced propagules but did not re-establish themselves (Barrat-Segretain 1996, Barrat-Segretain et al. 1998). In a similar manner, fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* were both able to colonize new substrata after dislodgement, but the former was viable for a longer period of time and could disperse over greater distances (Hall et al. 2006). Fragmentation is also important to the success of many invasive aquatic plants. For example, *Mimulus guttatus* (Truscott et al. 2006) employs fragmentation and recolonization to rapidly spread downstream after unpredictable flood pulses. Rapid colonization by fragments explains the success of the seagrass *Posidonia oceanica* (Di Carlo et al. 2005) and the seaweed *Caulerpa taxifolia* (Smith and Walters 1999) in the Mediterranean Sea.

Among animals, clonal taxa (e.g. cnidarians) or those with indeterminate integration of body plan (e.g. sponges) also adopt fragmentation as a strategy for reproduction and dispersal (Tunnicliffe 1981, Lasker 1984, Wulff 1991). Fragmentation provides particular benefits to corals and sponges that grow on coral reefs. Coral fragments exhibit higher survivorship than settling coral larvae (Highsmith 1982), and fragments of corals and sponges are able to repopulate substrata more quickly after disturbances such as storm damage (Highsmith 1982, Wulff 1995). Because most coral diseases are spread by contact with infected tissue, it has been suggested that fragmentation may be a mechanism for colonies to limit the spread of disease (Highsmith 1982). Moreover, transplantation of coral fragments has been proposed as a method for repopulating degraded coral reefs (Shafir et al. 2001).

Sponges are dominant members of the benthic community on Caribbean coral reefs (Targett and Schmahl 1984, Aronson et al. 2002, Maliao et al. 2008). Only a few studies have addressed asexual reproduction in Caribbean sponges, particularly the concept that a branching morphology may enhance fragmentation (Wulff 1991, 1995). Tsurumi and Reiswig (1997) noted that the production of propagules was very infrequent in *Aplysina cauliformis*, a thinly branching sponge, and suggested that the branching morphology may be an adaptation for fragmentation, but they did not compare propagule production in *A. cauliformis* with that of non-branching congeners.

Callyspongia armigera and *C. vaginalis* are two very common sponges on Caribbean reefs. The former grows as a branching gray rope, while the latter grows in clusters of gray tubes. Both species brood and release identical-looking, ciliated parenchymella larvae, ~0.5 mm in length, which are assumed to be sexual products. However, sperm have never been observed in histological sections of either species (Discussion) leaving open the possibility that the putative larvae are asexual products; therefore, they will be referred to herein as propagules. Propagules of both species swim up into the water column after release from the sponge, and disperse widely (Lindquist and Hay 1996, Lindquist et al. 1997, Pawlik unpubl.). Branches of *C. armigera* grow in all directions, forming clumps that attach readily when they come into contact with the substratum or with other branching sponges or gorgonian corals. Fragmentation of this species can be observed after attack by predatory fishes (particularly French and gray angelfishes, *Pomacanthus paru* and *P. arcuatus;* Pawlik unpubl.). Contrarily, tubes of *C. vaginalis* cannot reattach to the substratum, and dead or dying specimens can be seen tumbling over the reef after storms. To determine whether there is a resource tradeoff for *C. armigera* relative to *C. vaginalis*, we examined rates of growth and propagule production for each. We also documented the number of points of attachment per individual sponge for each species as an indication of their propensity to fragment. Life history theory predicts that if resources are limited and partitioned, a species that reproduces primarily through fragmentation should grow faster, but produce fewer propagules as a consequence.

Material and methods

Growth experiments were conducted off Key Largo, Florida, USA, at North Dry Rocks (25°07’850”N, 80°17’521”W) and Carysfort Reef (25°12’860”N, 80°12’810”W), with additional collections of material for reproductive output from Conch Wall (24°56’440”N, 80°27’230”W). North Dry Rocks is a shallow patch reef at 8 m depth. Conch Wall and Carysfort Reef are shallow reef flats, at approximately 12 m depth. Both sites are typical for long stretches of hard-bottom reef in the Florida Keys, where the predominant substratum is limestone pavement interspersed with small patches of overlying sand.

A survey was conducted at North Dry Rocks to determine relative abundances of each sponge species. Ten 20 × 5 m band-transects were surveyed along a continuous transect line and the number of sponge individuals of each species that lay within the band was recorded. Sponges that grew as a connected mass were counted as individuals. From the same transects, the number of points of attachment to the substratum for each individual sponge was counted as a measure of the ability of each species to reattach, and as a proxy for the propensity of each species to fragment. Examples of attachment substrata included surfaces that provided a firm anchor, usually limestone, pavement or dead coral, but sometimes other organisms, such as gorgonians and other sponges.

Growth data were obtained from eight predator-exclusion experiments conducted at North Dry Rocks or Carysfort Reef between 1996 and 2007. The experimental start dates were 6 May 1996, 19 May 1997, 12 May 1999, 6 May 2000, 7 May 2002, 5 June 2003, 25 May 2006 and 4 June 2007. Each experiment lasted 124 to 176 days. For each experiment and each species, 20 cube-shaped cages, 40 cm on a side, were constructed of vexar plastic mesh having 2 cm^2 openings and cable ties and secured onto the limestone substratum with nails. Sponge pieces (~ 40 g wet mass) were carefully collected from the surrounding reef by slicing fragments off healthy sponges with a scalpel; pieces were weighed on an electronic scale, tagged, returned to the same reef and secured with a cable tie to a brick inside the cages. At the end of the experiment, sponge pieces were retrieved and weighed in the same way. Growth rates were measured as a change in mass presented as a percentage of initial mass, and corrected for duration by dividing by the number of days of each experiment. Only sponge pieces that remained at the end of the experiment were included in analyses because it could not be determined whether missing pieces had died or been swept away; this left a total of 91 out of 100 and 53 out of 60 fragments of *Callyspongia armigera* and *C. vaginalis*, respectively. Data from different years were combined because there was no significant year effect for these two species in a larger analysis of sponge growth (Leong and Pawlik unpubl.).

To determine reproductive output, five sponges of each species were collected monthly from Conch Wall in Key Largo and processed for histology. Because reproductive timing can differ, even for species growing under the same environmental conditions (Riesgo and Maldonado 2008), samples were collected over an entire year from November 2007 to October 2008. Three cubes of tissue, ~1 cm on a side, were cut from each specimen, and immediately fixed in 4% formaldehyde in buffered sea water. Specimens were then rinsed with buffer and deionized water, dehydrated in solutions of increasing concentrations of ethanol (50%, 70%, 95%, 100%), and embedded in paraffin using toluene as a clearing agent. Using a rotary microtome, 10 μm sections were made and stained with haematoxylin and eosin. Sections were viewed and photographed with a microscope with an attached camera. A total of 20 views of each specimen were haphazardly photographed at 4× magnification to give a total scanned area of 130 mm^2 for each sponge. The surface area of any propagules present was quantified using the image analysis software ImageJ (Rasband 1997). Surface area measurements were then converted to a percentage of the total surface area, termed the reproductive output index (ROI; Whalan et al. 2007), which was used to compare relative reproductive output between species.

Two- and one-tailed Student's t-tests were used to compare differences in abundance and growth respectively, for each sponge species. Because the data were not normally distributed ($p < 0.001$; Shapiro–Wilk test), the non-parametric Kruskal–Wallis test was used to determine the significance of differences in numbers of attachment points and numbers of propagules between the two sponge species.

Results

In surveys of North Dry Rocks reef off Key Largo, Florida, there was no significant difference in the abundance of *Callyspongia armigera* and *C. vaginalis*, with mean values of 11.9 and 10.1 sponges per transect, respectively (two-tailed t-test, $t = 2.101$, $DF = 18$, $p = 0.2471$; Fig. 1). *Callyspongia armigera* had an average of 2.22 attachments per individual sponge, which was significantly more than 1.03 attachments per individual for *C. vaginalis* (Kruskal–Wallis, $\chi^2 = 113.86$, $DF = 1$, $p < 0.0001$; Fig. 2).

Sponge growth in predator-exclusion experiments was over four times higher for *C. armigera* ($n = 91$, mean $= 0.358\%$ initial mass day^{-1}) than for *C. vaginalis* ($n = 53$, mean $= 0.079\%$ initial mass day^{-1}; one-tailed t-test, $t = 6.395$, $p < 0.0001$; Fig. 3).

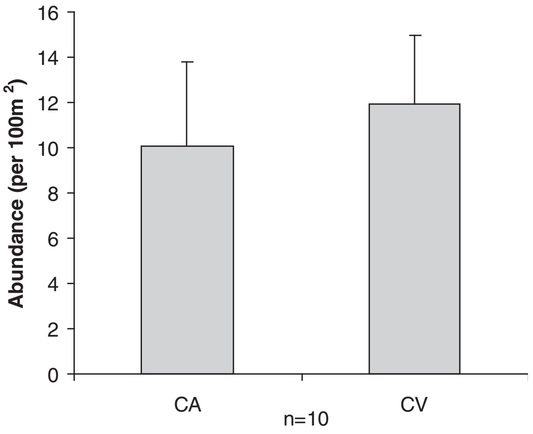

Figure 1. Abundance of *Callyspongia armigera* (CA) and *Callyspongia vaginalis* (CV) from band transects at North Dry Rocks reef, Key Largo, Florida. Mean + SD, n = 10.

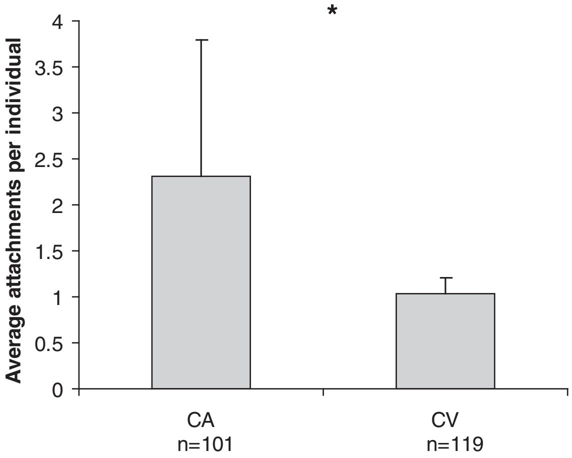

Figure 2. Average number of attachments per sponge for *Callyspongia armigera* (CA) and *Callyspongia vaginalis* (CV) from band transects at North Dry Rocks reef, Key Largo, Florida. Mean + SD, n = 101 and 119 respectively. Asterisk indicates a significant difference in the number of attachment points (Kruskal–Wallis, $p < 0.0001$).

Both *C. armigera* and *C. vaginalis* brood their propagules in distinct chambers within the sponge tissue. Propagules appear identical for both species, are ~0.5mm in length and can be easily seen without magnification. When reproductive propagules were present in an individual sponge, the ROI was comparable between species (1.22 for *C. armigera* and 1.78 for *C. vaginalis*). After monthly samples for one year ($n = 60$), only two reproductive individuals of *C. armigera* were found, one in March and another in October 2008 (Fig. 5). On the other hand, 18 of 60 samples (30%) of *C. vaginalis* exhibited propagules, and there was apparent seasonality in their production, with propagules found in December 2007, and from May to September 2008 (Fig. 5). No sperm were observed in any tissue sample. Overall,

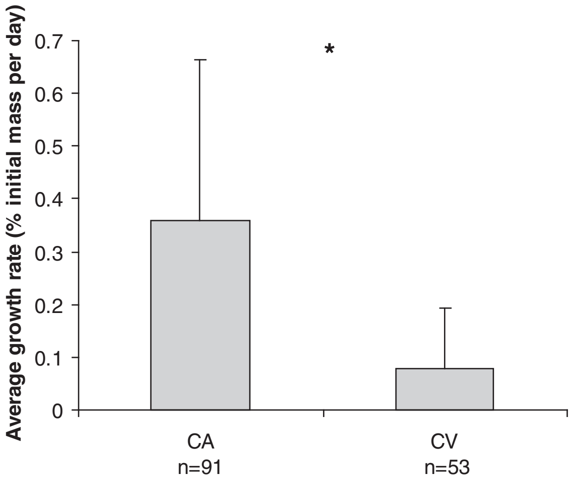

Figure 3. Relative growth of *Callyspongia armigera* (CA) and *Callyspongia vaginalis* (CV) as percentage wet mass increase day^{-1} from eight caging experiments conducted at North Dry Rocks, Key Largo, Florida from 1996 to 2007. Mean + SD, n = 91 and 53 respectively. Asterisk indicates a significant difference in mean growth (t-test, $p < 0.0001$).

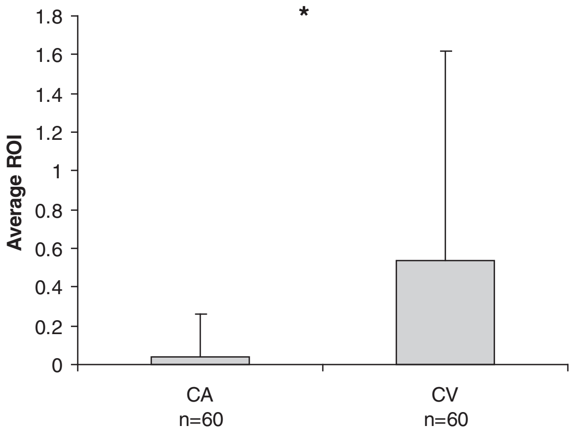

Figure 4. Mean reproductive output of *Callyspongia armigera* and *Callyspongia vaginalis* from Conch Wall, Key Largo, Florida for November 2007 to October 2008. Mean + SD, n = 60. Asterisk indicates a significant difference in ROI (Kruskal–Wallis, $p < 0.0001$).

C. armigera had a significantly lower average annual ROI than *C. vaginalis* (Kruskal–Wallis, $\chi^2 = 15.317$, $p < 0.0001$; Fig. 4).

Discussion

As for some aquatic plants (Barrat-Segretain 1996, Barrat-Segretain et al. 1998, Hall et al. 2006), our data support a resource tradeoff between investment in growth and fragmentation versus propagule formation for *Callyspongia armigera* relative to *C. vaginalis*, both of which are equally abundant on reefs off Key Largo, Florida. By reproducing primarily through fragmentation, *C. armigera* can quickly colonize free substrata after damage due to fish predation or disruption caused by storms, that occur frequently along the Florida reef tract. Contrarily, *Callyspongia vaginalis* relies primarily on propagule formation for reproduction, with the likely benefits associated with greater dispersal potential and sexual recombination.

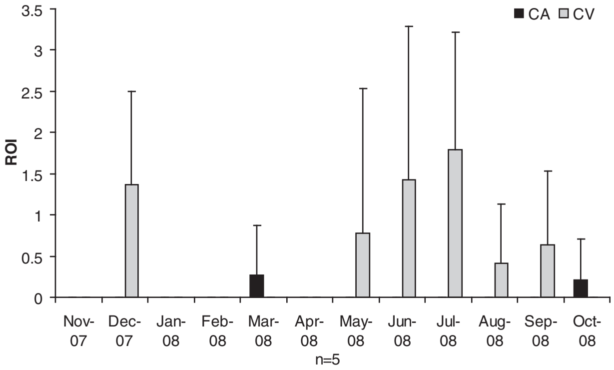

Figure 5. Mean monthly reproductive output index (percentage area propagules) of *Callyspongia armigera* (CA) and *Callyspongia vaginalis* (CV) from Conch Wall, Key Largo, Florida for November 2007 to October 2008. Mean + SD, n = 5.

Besides sponges, there are other Caribbean reef invertebrates for which a branching growth form is thought to be advantageous for reproduction by fragmentation. The gorgonian *Plexaura* sp. (Lasker 1984) and staghorn coral *Acropora cervicornis* (Tunnicliffe 1981) also reproduce primarily by clonal fragmentation, with little evidence of propagule formation. Similarly, fragmentation is the primary mode of reproduction in arborescent and vine-like bryozoans (Thomsen and Hakansson 1995), and levels of genetic diversity suggest that asexual fragmentation dominates among branching reef-building corals on the Great Barrier Reef (Ayre and Hughes 2000). Interestingly, for the Mediterranean sponge *Scopalina lophyropoda*, it has been proposed that fragmentation may enhance dispersal of propagules, because very small sponge fragments contain and nourish developing embryos (Maldonado and Uriz 1999), but a similar situation does not occur in *Callyspongia* spp., which have large brood chambers loosely packed with propagules.

Fragmentation is often cited as an evolutionary alternative to sexual reproduction (Tunnicliffe 1981, Lasker 1984, Wulff 1991, Thomsen and Håkansson 1995, Ayre and Hughes 2000, Sherman et al. 2006), and for plants, should be favored in stable, unchanging environments (Abrahamson 1975, Silvertown 2008). This seems contrary to the foregoing discussion of sponge fragmentation requiring disturbance events to break sponges apart and disperse them prior to recolonization. Indeed, without some level of disturbance, sponge fragmentation would not occur. For another Caribbean reef invertebrate, the gorgonian coral *Plexaura kuna*, a generalized model relating fragmentation, population structure and disturbance was proposed by Coffroth and Lasker (1998). They found the greatest evidence of reproduction by fragmentation, and the lowest genotypic diversity, at intermediate levels of disturbance (Coffroth and Lasker 1998). A similar model may be useful in describing the relative abundances of the two species of *Callyspongia*: while *C. vaginalis* is common on most reefs, *C. armigera* is abundant only on reefs that experience low to moderate currents and have high topographic complexity (coral rubble). While propagules of both species are likely to disperse to most reefs, strong currents on some reefs may flush away fragments of *C. armigera*, particularly if low habitat complexity does not provide microhabitats where fragments can settle long enough to attach.

The present study did not attempt a demographic analysis of *C. armigera* and *C. vaginalis* to quantify their respective dependence on fragmentation and larval recruitment, as this would require long-term monitoring and tagging of sponges. Instead, several lines of evidence support our assumptions about the life-history differences of the two species. Not only is there abundant evidence of fragmentation of *C. armigera* in the field, it can be observed occurring when sponge-eating fishes attack this species and leave behind partially eaten branches (Pawlik unpubl.). Similar attacks on *C. vaginalis* leave behind holes in the tubes, which regenerate rapidly (Walters and Pawlik 2005), but with no dislodgement of the firmly attached sponge. After even moderate storm events, clusters of branches of *C. armigera* were broken-up, with only remnant branches at the initial sites of attachment, and torn branches scattered and attached about the reef. Individual tubes or tube clusters of *C. vaginalis* usually survived these storms intact, but when dislodged, were observed to be dead or dying in the sand channels between the reefs, and are often washed ashore in the beach wrack (Pawlik unpubl.). Because *C. vaginalis* grow with their tubes and osculae oriented upward, reattachment of this species would lead to haphazard re-orientation, and this has not been observed in the field. Quantification of attachment points for the two species (Fig. 2) support the qualitative evidence for fragmentation vs. reproduction for *C. armigera* and *C. vaginalis*, with more than a two-fold mean difference between the two species, and much higher variance for *C. armigera* reflecting the haphazard effects of predation and disturbance. The narrow variance around 1.0 attachment points per sponge for *C. vaginalis* is further evidence that this species grows from the single point of propagule settlement and subsequent growth.

Callyspongia armigera and *C. vaginalis* are not the only *Callyspongia* species found on reefs in the Florida Keys. *Callyspongia fallax* and *C. plicifera* also occur, but in much lower abundances. Although reproductive data are lacking for these species, inspection for brood chambers suggest that they are less fecund than *C. vaginalis* (Pawlik unpubl.), but like *C. vaginalis*, they are both tube sponges and do not fragment and reattach like *C. armigera*. A combination of low reproductive output and the absence of asexual reproduction by fragmentation for *C. fallax* and *C. plicifera* may explain their low abundance on Caribbean reefs.

Interestingly, sperm were not observed in histological sections from tissues of either *C. armigera* or *C. vaginalis,* leaving some question as to whether propagules are sexual or asexual products. Asexual production of larvae in marine sponges could not be discounted in other studies (Ilan and Loya 1990). Sperm have been absent in some studies of sponge reproduction (Fell 1989, Corriero et al. 1996), while in others, heavily skewed sex ratios for both females (Tsurumi and Reiswig 1997, Mercurio et al. 2007) and males (Whalan et al. 2007) have been reported. However, it is more likely that sperm may be produced diffusely in these species, making them unrecognizable by light microscopy, or that the time between sperm development and release is so short that a monthly sampling scheme would overlook their presence (Mercurio et al. 2007).

Our study provides the first comparative evidence that there is a tradeoff between growth and propagule formation in closely related coral reef sponges that exhibit differences in morphology and capacity to fragment. This is likely only one of several tradeoffs in the resource budgets of Caribbean reef sponges, which may also include wound-healing after grazing by sponge-eating fishes (Walters and Pawlik 2005), and investment in chemical defenses to deter predation (Pawlik et al. 1995, Pawlik 1997, 1998). Experimental evidence for these tradeoffs is forthcoming (Leong and Pawlik unpubl.), but compelling support for the tradeoff between chemical defense and growth or reproduction is evident in the community succession of sponge recruitment into new habitat provided by an artificial reef shipwreck (Pawlik et al. 2008). It appears that the species that make up Caribbean reef sponge communities have taken very different evolutionary trajectories in allocating metabolic resources to growth, reproduction and chemical defense.

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