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Bonsai anemones: Growth suppression of sea anemones by their associated kleptoparasitic boxer crab

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Highlights

- We studied the nature of the association between a boxer crab and sea anemones.
- Crabs minimize anemone's contact with food.
- Precise removal of food particles from anemones
- Anemones reared away from the crabs grew significantly.
- Anemone growth is regulated by crab kleptoparasitic behavior.

Abstract

Kleptoparasitism, the theft of food, is a foraging strategy often overlooked or misinterpreted as a commensal association. Crabs of the genus *Lybia*, commonly known as boxer crabs, hold a pair of tiny sea anemones in their claws. The nature of this seemingly commensal association has never been tested empirically. In a laboratory study of food consumption, we show that the boxer crabs *Lybia leptochelis* regulate the size of their claw-held sea anemones (*Alicia* sp.). The anemone size is regulated by: (a) distancing the held anemones from presented food – and in the event any food particles are caught – (b) using rapid leg movements to remove most of the food captured by either anemone. Anemones removed from the crabs and grown independently underwent remarkable changes in morphology, color, and size, with over 250% expansion in pedal-disk diameter. The ultimate aim of classical kleptoparasitism is food acquisition by the pirate. We have shown a completely new role of kleptoparasitism, in which the victim is not only robbed of food, but is also regulated in size. The boxer crab thus maintains a “Bonsai” symbiont that is conveniently carried around as a tool to trap its food and provide protection.

Introduction

Kleptoparasitism, the theft of food collected by another individual, is one of the most widespread forms of exploitation (Barnard, 1984). It is well documented not only for birds (Barnard, 1984, Brockmann and Barnard, 1979, Furness, 1987, Yosef et al., 2011), but also for mammals (Gorman et al., 1998), fish (Dominey and Snyder, 1988), reptiles (Cooper and Perez-Mellado, 2003), a wide range of invertebrates (Fratini et al., 2011, Iyengar, 2002, LaPierre et al., 2007, Morissette and Himmelman, 2000, Vollrath, 1984) and other members of the animal kingdom (see Iyengar, 2008 for a comprehensive review). It has been shown that, if successful, kleptoparasitism is more advantageous than foraging or predation, often saving much time and effort (Iyengar, 2002, Morand-Ferron et al., 2007, Yosef et al., 2011). Such associations may be facultative or obligatory on the part of the kleptoparasites (Iyengar, 2008).

Kleptoparasitism can also be a major driving force in the evolution of the morphology and behavior of the participants, as hosts and kleptoparasites respond to the selective forces exerted by each other (Iyengar, 2008, Tso and Severinghaus, 1998). For example, in some slave-making ant species, an extreme form of kleptoparasitism, the masters are incapable of feeding themselves and so would go extinct without slaves (Iyengar, 2008). Furthermore, when the theft of food occurs in closely-associated symbiotic species, such as spiders stealing food from other spiders, the kleptoparasite is often the smaller and more stealthful of the two species (Iyengar, 2008, Vollrath, 1984). The focus of most studies is on the kleptoparasite, and little attention is paid to the quantitative impact, in terms of food intake and growth, on the host. While such cases are limited, notable examples include kleptoparasitic snails (Iyengar, 2002, Iyengar, 2004, Pernet and Kohn, 1998) and spiders (Grostal and Walter, 1997), which affect to varying extents the growth of their hosts.

Boxer crabs of the genus *Lybia* carry a pair of small sea anemones or less commonly, nudibranchs, in their claws (Baba and Noda, 1993, Karplus et al., 1998). Previous studies have suggested that the crabs use the anemones and their toxin-releasing nematocysts as a living deterrent to predators and as a tool for obtaining food (Duerden, 1905, Karplus et al., 1998). Duerden (1905) observed that when presented with food, the crab would "rob" it from the anemone's mouth and in many cases remove all the food particles. The anemone's presumed benefit, as a primarily sessile animal, would come from the mobility the crab gives it (Duerden, 1905), giving the anemone further access to oxygen and its transport to further food sources (Karplus et al., 1998). The crab holds the anemone in highly adapted claws, which have specialized hooks that are slightly embedded in the anemone at all times (Guinot, 1976). These chelae have effectively lost their ability to function in a typical crab manner, as they are "slender and feeble — ill suited for defense, but at the same time mobile and well adapted to wield the anemones they carry" (Duerden, 1905). Indeed, there are no known instances of a *Lybia* crab being found without a pair of anemones, suggesting that this association is obligatory, at least on the part of the crab (Duerden, 1905, Karplus et al., 1998; personal observation). There is some anecdotal information in the literature suggesting that the crab affects the morphology of its captive associate. *Triactis producta*, the sea anemone held by *Lybia tesselata* is far smaller, and has almost no resemblance to its commonly occurring free-living form. The "crown" of outgrowths usually surrounding the lower part of the column in free-living *T. producta* is always absent in crab-held anemones (Cutress, 1977). Nudibranch sea slugs (*Gymnodoris* sp.) held by *Lybia hatagumoana* are smaller and have degenerated external gills compared to free-ranging Gymnodorids (Baba and Noda, 1993). It has been suggested that these differences arise as a consequence of being held by the crab (Cutress, 1977, Karplus et al., 1998). However, there has been no experimental demonstration of the mechanism involved in these morphological alternations.

The aim of this study was to answer two broad questions: (1) Does the crab indeed steal food acquired by the anemones it holds? (2) How are the anemones affected by being carried constantly by the crab, particularly with regard to growth?

To this end, we conducted a feeding and growth experiment on the locally occurring *Lybia leptochelis*, holding anemones of the genus *Alicia*.

Crab-invertebrate (e.g. cnidarians) associations are generally regarded as commensal, and in virtually all cases studied the crab is the smaller of the two associates (Thiel and Baeza, 2001). This is therefore an unusual association in which the crab is the larger of the two associates. The experiment was grounded on the postulate that if the amount of food consumed by the crabs and anemones when fed alone equals the amount they consume when they are in their normal associated state, this might indicate that the relationship between them is mutualistic or commensalistic. However, if the amount consumed by the anemones in association is lower from that when they are separated, this would indicate that they are being deprived by the crabs and that the partnership tends to approach a kleptoparasitic interaction. Furthermore, little attention has been paid to the factors underlying the size and morphological differences between held and free living anemones of the same species. Therefore, the growth of crab-held and freely reared anemones was quantified over the course of the feeding experiment and beyond it.

Section snippets

Collection of animals

Living specimens of *L. leptochelis* and their symbiotic *Alicia* sp. sea anemones were collected in the summer of 2007. Only fully intact crabs were collected. Oviparous females were not collected. Using a small hand-held net, the crabs were taken from under rocks below the low tide zone just south of the oil terminal compound in the Gulf of Eilat. They were then individually placed in 0.5L bottles filled with fresh sea water from the collection site, kept in a thermally insulated box and…

Results

The free anemones consumed between 0.5 and 4 *Artemia*, on average, per session over the course of the experiment (Fig.2a). Their morphology changed dramatically, colors became more vivid, and the diameter of their PD increased up to over 250%, as compared with those held by crabs (See Table1; Fig.1, Fig.2b; Supplementary material, Fig.1A). The regression model shows that the free and fed anemones grew significantly, with an average size increase of 177% over the course of the experiment…

Discussion

The relationship between *L. leptochelis* and *Alicia* sp. is an extreme example of a kleptoparasitic interaction: *Lybia* interacts with its anemones by preserving their minute size by food reduction, much as gardeners produce "Bonsai" trees, effectively maintaining the anemones to use at its will. Anemones removed from the crabs grew considerably (Fig. 1), some attaining sizes much greater than the crabs from which they were taken. To our knowledge, there is little evidence suggesting an effect on…

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