Attack Autotomy: A Defense against Predators

Abstract. *The response of five species of crabs to simulated predator attack was examined. Two terrestrial species autotomized their chelipeds after the chelae were firmly attached to the predator. Selection for attack autotomy is balanced by selection for retention of the cheliped whenever the cheliped is important in social or maintenance functions.*

Of the defensive activities found in the animal kingdom, two are normally unlikely to occur simultaneously; attack, involving the use of weapons (teeth, claws, spines, or stings), and escape or withdrawal to a protected position (*1*). Observations on encounters between a tame Central American otter (*Lutra annectens*) and freshwater crabs (*Potamocarcinus richmondi*) suggested that crabs may effectively combine these two types of defense. On two occasions, when hunting along freshwater streams, the otter, an immature male, was seen to attack the crab *P. richmondi*. The first attack took place under water. The otter made a swift lunge at a retreating crab and almost immediately emerged from the pool uttering a series of high-pitched distress calls, with the right cheliped of the crab firmly attached to the loose folds of skin beneath its neck. The second encounter took place on land. The otter attacked a crab that was retreating toward a rock fissure. The crab's cheliped was detached onto the right forefoot of the otter, which then fled to a nearby pool, while the crab escaped into the fissure. We detached the powerfully closed chela from the otter some 2 minutes later.

These observations suggest that the crab may autotomize a counterattacking weapon while it is attached to the attacker and escape while the predator is still dealing with a painful attack. We found only one brief note on the occurrence of attack autotomy in other species of crabs, and this gives no details about the frequency of occurrence or the situations in which it occurs (*2*).

To investigate this phenomenon in more detail we made simulated attacks on crabs of five species that occur abundantly in Central America. These species ranged in habitat from intertidal to terrestrial and freshwater. As a "predator" we used a child's toy teddy bear mounted on a wire (1 m long). The bear was about 30-cm long with a crude mammalian surface texture and profile and was effective in eliciting defensive behavior. Attacks were made on crabs in their normal habitats during the day and night. *Cardisoma crassum*, a hole-dwelling species, could not be approached closely enough to attack. They were collected and attacked in a large (4 by 4 m) mud-floored arena in the laboratory. When a crab was discovered, the bear operator stepped back, crouched down, and presented the anterior portion of the bear for 30 seconds, pushing it forward into contact with the crab. The bear was then sharply withdrawn to simulate the retreat of the predator. The response of the crab was recorded at each stage of the encounter. Whenever possible, the crab was captured and measured, and its sex determined (Table 1). If the crab detached a cheliped during the attack phase, this was regarded as active autotomy, because a tensile force was not exerted by the bear operator on the cheliped. Autotomy occurring during withdrawal was regarded as passive autotomy, because the chela was being pulled by the withdrawal movement. After autotomy, the fingers remained in tonic contraction for several minutes.

Of the five species of crabs studied, only two, *Potamocarcinus richmondi* and *Gecarcinus quadratus*, autotomized readily during the attack phase. *Potamocarcinus richmondi* inhabits freshwater streams and wet areas of forest. At the approach of a predator, the crabs displayed, raising the carapace anteriorly and stretching the pereiopods, so that the fifth pair was directed backward acting as a brace. The chelipeds were oriented toward the predator. When attacked by the predator, the chelae snapped and closed on the ears or legs of the bear. Twenty-three of the 41 crabs attacked with the bear autotomized one or more chelipeds during the first moments of counterattacking. When the bear was withdrawn sharply, nine chelipeds were autotomized. Eleven of the crabs autotomized both chelipeds. In nine cases autotomy did not occur; two of these had previously lost one cheliped and the remaining seven were very large adults.

Gecarcinus quadratus inhabits the grassy areas high above the tide line on the Pacific coast of Panama, hiding under stones during the day and foraging in exposed areas at night. When the stone or log was raised during the day *G. quadratus* ran toward the nearest cover, raising its chelipeds and exposing the inner white surface as it ran. When cornered, both by day and night, it assumed a threat posture, similar to that of *P. richmondi*, and in 17 out of 30 encounters the crab stridulated (*3*). When attacked by the bear, 20 of the crabs autotomized at least one cheliped at the moment when the fingers closed on the predator (Fig. 1), and nine of them autotomized when the predator retreated. Ten of the crabs autotomized both chelipeds. Four crabs did not autotomize either cheliped, and we have no indication of any correlation between size and readiness to autotomize.

We found *Cardisoma crassum* living in burrows on mud flats by streams of brackish water. When attacked with the bear in the laboratory arena, they raised the anterior edge of the cara-

Table 1. Species of crabs and response to disturbance and attack (*9*).

Species	Response to disturbance					Response to attack				
	Display	Stridulation	Retreat into burrow	Escape by running	Assume cryptic position	Counterattack	Active autotomy	Passive autotomy	Autotomy of both chelae	Crabs (No.)
*P. richmondi**	33			22		34	23	9	11	41
G. quadratus†	28	17		4		26	20	9	10	30
C. crassum‡										46
C. crassum‡	6§		46			6§		1§		6§
E. squamata ‖	23			15	2	22		4		25
X. sternberghii ‖	1			33	127					160

* Freshwater and terrestrial; from Barro Colorado Island, Canal Zone. † Terrestrial, from Naos Island, Canal Zone. ‡ Terrestrial, in burrows, from Albrook, Canal Zone. § Encounters took place in the laboratory. ‖ Intertidal, from Paitilla Point, Republic of Panama.

Fig. 1. "Predator" with two chelipeds of *Gecarcinus quadratus* autotomized on its face. [Photo by D. Farrell]

pace and oriented their chelipeds toward the threat, closing their chelae on the bear. No amount of shaking or sharp withdrawals induced autotomy. However, when one of us tried to pull a crab out of its burrow by its cheliped, the cheliped was autotomized (*4*).

Eriphia squamata and *Xanthodius sternberghii* are both found in the intertidal zone, *E. squamata* under stones and in shallow pools and *X. sternberghii* under stones. When *E. squamata* was disturbed, 15 out of 25 crabs encountered ran for cover, holding the chelae above the carapace and displaying. The display was similar to the startle display of many insects (*1*) with the chelipeds maximally extended laterally; this display increases their apparent size and reveals the striking coloration of the inner surfaces and of the bright red fingers. When cornered and attacked, 23 crabs displayed and counterattacked by "biting." Autotomy did not occur during the attack, but four crabs autotomized when the bear was sharply withdrawn.

Xanthodius sternberghii are extremely cryptic and, when first exposed or disturbed, remain motionless with their legs curled under them (*5*). Of the 160 crabs exposed, 127 remained motionless for more than 1 minute. The crabs then slowly edged for cover or almost imperceptibly dug into the sand. Thirty-three of the crabs ran as their initial response to disturbance; one large male displayed, holding both chelipeds over the carapace as it ran for cover. It was not possible to induce counterattacks on the predator, and when *X. sternberghii* was held in the hand, 42 out of 52 crabs feigned death.

The evolution of attack autotomy may be a factor which allows the terrestrial crab to defend itself effectively while wandering far from a burrow or retreat. Mammals which may be vulnerable to attack autotomy include otters, raccoons, and opossums, all of which occur in the crabs' habitats and are known to feed on crabs (*6*). Although the encounters between the otter and *P. richmondi* show that the autotomy of the attacking weapon is a successful form of defense, defense is not the only function of the chelipeds. Selection for retaining the cheliped will be exerted wherever this organ is important for functions other than defense. In gregarious intertidal and terrestrial crabs, the chelipeds may have acquired important functions in social signaling and fighting (*7*). In addition, the diet of the crab may affect the importance of the cheliped for feeding purposes and its consequent disposability. Some crabs can learn to feed effectively by using their walking legs (*8*), and *P. richmondi* and *G. quadratus* have been observed feeding on fallen fruit which does not require the use of chelipeds.

Autotomy, in the broad sense, in other arthropods and reptiles (and the autotomy of walking legs in crustaceans) permits the escape of the prey only if the predator chances to seize an autotomizable part. Active autotomy, as we have described it in *P. richmondi* and *G. quadratus*, is a process by which the active role belongs to the potential prey and the defense does not depend on the chance orientation of the predator's grasp.

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References and Notes

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2. H. Schöne, *The Physiology of Crustacea* (Academic Press, New York, 1961), p. 474.
3. L. G. Abele, M. H. Robinson, B. Robinson, in preparation.
4. To test the response of *C. crassum* to predators in the field, we glided a black hawk model over the colony and pulled the toy bear across it on a piece of string. When the model was flown over the colony at a height of 1.2 m, all the crabs in a 1.8-m path below the flight path retreated down their holes. The first crabs appeared after 1 minute at the first flight, 45 seconds after the second, and 30 seconds after the third flight. When the bear was dragged through the colony, crabs within 0.6 m went down their burrows, those between 0.6 and 0.9 m moved to the entrance, and beyond this there was no response.
5. J. Crane, *Zoologica (New York)* **32**, 76 (1947).
6. L. B. Holthuis, *Verh. Zool. Botan. Ges. Wein* **44**, 1 (1959).
7. H. Schöne, *Amer. Zool.* **8**, 641 (1968); H. O. Wright, *ibid.*, p. 655.
8. R. W. Hiatt, *Pac. Sci.* **2**, 135 (1948).
9. The attack was maintained for 30 seconds against all crabs except *E. squamata*, which was attacked for 1 minute. After 30 seconds the crabs usually became lethargic and would not respond.

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Reinforcement of Competing Behavior during Extinction

Abstract. *Conditioned behavior declines in frequency when reinforcement is discontinued. In two experiments this extinction process was facilitated when competing behavior was reinforced as the original response was extinguished. When reinforcement for competing behavior was withdrawn, however, rats resumed their original behavior and there were no overall savings in total responses to extinction.*

There are many ways to suppress behavior including physical restraint, satiation, punishment, and extinction. Restraint physically prevents the organism from engaging in the old behavior; satiation involves a procedure such as previous feeding and implies that the deprivation motivating the old behavior has been relieved; punishment involves the delivery of aversive stimuli following the old behavior; and extinction consists of the withdrawal of the former consequences (reinforcers) of the old behavior. Except for physical restraint, which hardly needs any refined analysis, each of these procedures has been studied extensively (*1*). A less frequently explored method for suppressing behavior involves reinforcing behavior incompatible with the old response (*2*). Terms such as competing behavior, reciprocal inhibition, interference, counterconditioning, and antagonistic responses refer to the same issue: How can performance of one behavior prevent the performance of another behavior?

Unfortunately, competing responses