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Intraspecific Deception by Bluffing: A Defense Strategy of Newly Molted Stomatopods (Arthropoda: Crustacea)

Abstract. *After molting, stomatopods can be evicted easily from home cavities by conspecifics because these marine crustaceans lose temporarily their body armor and the use of their raptorial appendages. Some newly molted stomatopods defend their cavities with a meral spread display, a signal correlated with attack when used by animals between molts. The use of the meral spread display actually increases after molting. Since new molts cannot fight, their use of meral spread appears to be a bluff.*

Animal studies have shown many deceptions used between species (*1*) but few examples from intraspecific interactions (*2, 3*). There is even a question of whether deception can be maintained in this context since it may be evolutionarily unstable (*2–4*). One form of deception is a bluff, where fighting ability or the tendency to persist in or escalate a contest is misrepresented. We report that newly molted individuals of the marine crustacean *Gonodactylus bredini* bluff conspecific opponents.

Gonodactylus bredini lives in the Caribbean and defends cavities in hard substrata. The second maxillipeds are enlarged to smash hard-shelled prey and, apparently in conjunction with the evolution of these weapons, *G. bredini* has evolved armor and a complex repertoire of agonistic displays that it uses during contests for cavities (*5*). Like other crustaceans, *G. bredini* molts to grow and repair the exoskeleton. After molting, the cuticle is soft for at least 3 days, providing little protection from predators or competitors (*6*), and the raptorial appendages are not effective for up to 4 days. Thus, molting periodically destroys a stomatopod's fighting ability or resource holding power (RHP) (*7*).

Table 1. Cavity defense tactics used by *G. bredini* residents during day 1 contests. After an intruder is detected, residents either flee or stay and attempt to retain the cavity. If they remain, residents hide deep inside the cavity and give no displays, or they actively defend the cavity by displaying to intruders.

Tactic	Won	Lost	Total
	New molts		
Flee		13	13
Hide	7	23	30
Display	9	8	17
	Controls		
Flee		1	1
Hide	2	3	5
Display	17	2	19

Because maintenance of a home cavity dominates the biology of gonodactylids, we examined how newly molted residents defend cavities and how aggressive behavior changes as RHP returns. Each new molt ($N = 60$) was placed into an arena 30 cm in diameter with a piece of coral rubble, where it established residency in a cavity that a stomatopod of similar size had occupied in the field. Less than 12 hours after the resident had molted (day 1), we introduced an intruder that was between molts (intermolt) into the arena and recorded the interaction until one of the contestants left the vicinity of the cavity. Trials against different intruders were staged on days 2, 3, 4, 5, 7, and 10. Intermolts ($N = 25$) were used as residents for the control series. All opponents were matched according to their size and sex. The data were pooled for males and females since we detected no differences in their behavior. On average, 74 percent of controls retained their cavities during a contest. New molts were less successful on days 1 through 5 (*G*-test; all $P < 0.05$) (*8*) but recovered RHP at least to premolt levels 7 to 10 days after ecdysis.

Some new molts were able to retain their cavities only hours after ecdysis by aggressively displaying to intruders (Table 1) (*9*). Residents that display typically use five agonistic acts: appear, lunge, meral spread, strike-cavity, and strike-opponent (Fig. 1). Controls tended to attack and used strike-opponent most frequently. New molts, which could not strike, used meral spread in 15 out of 17 contests while controls used it in only 4 of 19 contests (*G*-test, $P < 0.001$) (*10*). These new molts apparently were attempting to defend their cavities by bluffing.

To present a meral spread, *G. bredini* and other gonodactylids lean out of their cavity and while facing an opponent, raise and laterally spread the raptorial appendages. At times, the magnitude of the spread is increased during an exchange. Meral spread by intermolts has been described as a conventional threat display and linked statistically to escalation by the signaler and to inhibition of attack in opponents (*5*). Meral spread provides information about size that intruders could use to assess fighting ability. The data on subsequent behavior and the sometimes graded nature of the display indicate that meral spread also may signal motivation. Regardless of whether meral spread signals the tendency to fight or fighting ability, or both, a new molt cannot fight and its use of meral spread must be a bluff. The increased frequency of meral spread implies that a bluff is an important defensive tactic for new molts.

The sequences of behavior support the conclusion of attempted deception. Fifteen new molts met intruders with a full intensity meral spread and two lunged at the opponent first. Four new molts also lunged immediately after the meral spread. Either action caused intruders to coil in a defensive posture, shielded by their armored telsons. Nine intruders then swam away rapidly. The other intruders continued to approach, causing all the new molts in these instances to leave their cavities. Not one displaying new molt persisted if its bluff was called (*11*).

These bluffs operate by exploiting a visual signal. For many animals, displays such as meral spread contain information about size, which indicates fighting ability; they are therefore resistant to cheating (*3*). Small differences in size can affect the outcome of contests between intermolt stomatopods (*12*), apparently by determining the size of the raptorial appendages and thus the potential force of a strike. Meral spread contains accurate information about size, both of the weapons and their bearer. Molting, however, causes these weapons to be ineffective temporarily and introduces variation into the reliability of the visual signal that cannot be immediately detected (*13*). This hidden variation allows new molts to subvert the meral spread since they are not bluffing size itself but the correlation between the size of their raptorial appendages and the typical effectiveness of those weapons.

Bluffing appears to be a successful tactic because probing may be costly for an intruder. Gonodactylid stomatopods can cause serious injury with a single blow and several factors favor the residents during contests: (i) residents are not visible and assessment of their RHP is difficult; (ii) the cavity protects residents, while intruders, in the open, are more vulnerable to strikes; (iii) long contests increase the probability that the exposed intruder will attract predators. Furthermore, an intruder in the field is likely to have been evicted from its cavity because of reduced fighting ability brought about by molting or injury. Bluffing may be most successful against these intruders who are even more vulnerable to the risks of probing. We do not mean to imply that probing is not common, merely that some intruders act as if information gained from probing may be outweighed by the risks.

The percentage of meral spreads that are unreliable affects the evolutionary stability of the display. Our collection records for over 20,000 *G. bredini* in Panama indicate that most adults molt every other month. We estimate that in the population one resident in five (20.2 percent) using a meral spread would have molted in the past 5 days and be bluffing. That is, of the meral spreads encountered by an intruder, 80 percent would be from intermolt residents and should be reliable displays (*14*). Intruders would on average still benefit from any information derived from meral spread.

It is not clear why more new molt residents do not bluff. Perhaps, the proportion of bluffing is set within a mixed strategy where the frequency of each tactic is balanced by the success and associated danger of all options available. Whereas residents between molts can use the specialized weapons and armor, the options for cavity defense are restricted after molting. Thus, more new molts than intermolts flee (*G*-test, $P < 0.01$), and of those that remain, new molts tend to hide while intermolts interact agonistically with intruders (*G*-test, $P < 0.005$) (Table 1). Residents that flee avoid the cost of defense but give up their cavities. On the other hand, residents that hide occasionally retain cavities because some intruders are reluctant to probe an unseen opponent (*15*). But, hiding new molts are particularly vulnerable since they can be trapped and eaten (*16*). The last option is to defend the cavity. Intermolts tend to attack intruders in a variety of ways and were more successful when actively defending than when hiding (Fisher's exact test, $P = 0.04$). New molts that offered a defense could not attack but could attempt to bluff. However, the observed difference in success between new molts that hid and those that bluffed was not statistically significant (*G*-test, $P < 0.10$). Bluffing thus appears to be only one tactic within a framework of restricted options that offer limited success.

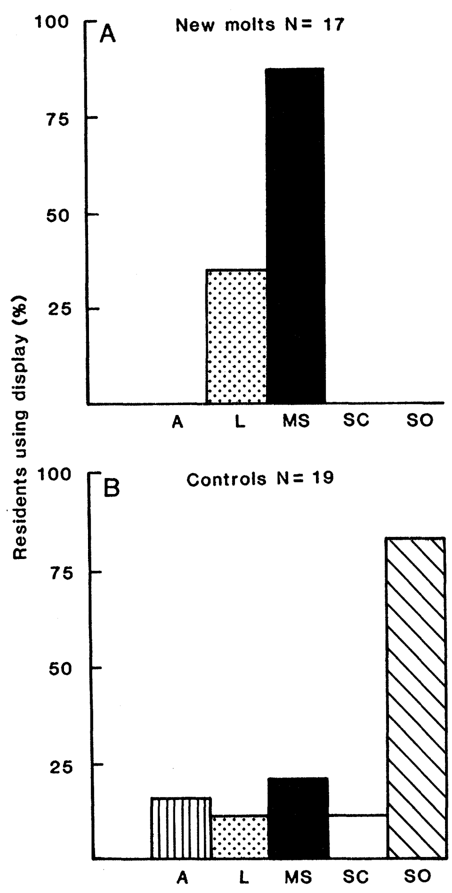

Fig. 1. Frequency of agonistic acts and displays by residents that attempted to defend their cavities during day 1 contests. Appear (*A*), with the resident stationed in the entrance, is a low intensity act, perhaps used in assessment and to advertise that the intruder has been detected. Lunge (*L*) is a rapid, headfirst movement toward the intruder, the resident does not leave the cavity completely nor does it strike. Meral spread (*MS*), characterized by a presentation of the raptorial appendages, is a conventional threat display (*5*), as is strike-cavity (*SC*), where a sharp blow to the inside of the cavity produces an audible click (*17*). Strike-opponent (*SO*) is an attack carried out with the raptorial weapons.

Some investigators argue that when a display affects the outcome of a contest it probably transmits information about fighting ability and not the signaler's "intention," since a signal that could settle a contest merely by indicating whether an animal will persist or escalate should be undermined by cheating (*3, 4*). Yet, data indicate that intermolt stomatopods may signal such tendency to fight by use of the meral spread (*5*). Perhaps the use of meral spread before an attack during the intermolt period lends credibility to this display that could be exploited during the period of postmolt vulnerability. An animal that uses meral spread but does not attack devalues the display for future encounters with its neighbors. The advantage gained by newly molted individuals that had reliably signaled attack when between molts would oppose the tendency for bluffs by intermolts to invade meral spread. *Gonodactylus bredini* is territorial and learns to recognize and to avoid more powerful individuals (*17*), which makes such speculation plausible (*18*).

Although the generality of intraspecific deception is still open to question, our findings suggest that deception during contests can persist within a population if there exists both risk from probing and hidden variation in an otherwise reliable assessment cue. Molting, common in many animals, can cause such variation (*19*).

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10. The frequencies of all acts were indistinguishable from control values by day 10.
11. Lunge may be part of the aggressive front of some new molts, but we chose conservatively to concentrate on the major component, meral spread.
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13. Intruders cannot detect newly molted residents visually since new molts easily fall within the wide range of intermolt color variations in *G. bredini*.
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15. Gonodactylids use chemical cues to detect and identify individual residents (*17*).
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Coronary Artery Spasm Induced in Atherosclerotic Miniature Swine

Abstract. *Angiographically demonstrable coronary artery spasm could be provoked repeatedly by giving intracoronary or intravenous injections of histamine to miniature swine with experimentally induced atherosclerotic lesions of the coronary artery. The spasm induced in this way subsided either spontaneously or after the administration of nitroglycerin and was prevented by a calcium antagonist or an agent that blocks histamine H_1 receptors. This model, which suggests that atherosclerotic changes may be one of the primary factors in the occurrence of coronary artery spasm, should facilitate studies on the pathogenesis of this condition.*

Coronary artery spasm causes not only variant angina but also certain forms of effort angina, acute myocardial infarction, and sudden death (*1*). Because the pathogenesis of coronary artery spasm is unknown, its prevention and treatment remain important clinical problems. However, the induction of coronary artery spasm in an animal model has not been successful. In the presence of severe stenosis, drastic coronary flow reduction may occur with minimal reduction in the stenotic area, probably not only as a result of physiologic changes in arterial tone but also because of minimal platelet aggregation. We therefore believe that an experimental model of coronary artery spasm should fulfill the following criteria: (i) no significant, angiographically demonstrable stenosis before induction of the spasm; (ii) transient and reproducible provocation of total or near total obstruction that can be documented by coronary arteriography; and (iii) regional myocardial ischemia in the spastic coronary territory.

We previously reported that experimentally induced atherosclerotic lesions in the canine coronary artery constrict more extensively with ergonovine than do non-atherosclerotic lesions in the same dog (*2*). We have now succeeded in provoking coronary artery spasm associated with ischemic electrocardiographic changes in miniature swine.

Fifteen male miniature swine (4 to 6 months of age) were fed on a diet containing 2 percent cholesterol after they were subjected to endothelial balloon-denudation of the left circumflex coronary artery. Such treatment promotes the development of selective coronary atherosclerotic lesions (*2, 3*). Before the denudation, and 1 and 3 months after the operation, selective coronary arteriography was repeated after intracoronary or intravenous administration of various vasoconstrictive agents, such as ergonovine (*4*), phenylephrine (*5*), histamine (*6*), and serotonin (*7*), all compounds that seem to be potent agents of coronary artery spasm in humans.

Coronary artery spasm in these experiments was defined as the transient excess vasoconstriction that subsides either spontaneously or after the administration of nitroglycerin and that is characterized by a decrease of over 75 percent in coronary diameter compared with that after the intravenous administration of nitroglycerin (20 μg/kg). Significant ischemic electrocardiographic changes were defined as more than 0.1 mV ST-segment elevation or depression from the control level. At the end of the experiments, intact and denuded portions of the left coronary arteries were examined histologically.

Coronary artery spasm was provoked repeatedly by intracoronary or intravenous administration of histamine, with or without cimetidine (a histamine-H_2 receptor blocking agent), in doses of 100 to 400 μg or 10 to 100 μg/kg, respectively (Fig. 1). The other three drugs were ineffective, except in one animal in which serotonin as well as histamine provoked the spasm. The spasm occurred only in the denuded portion of the left circumflex coronary artery, although the portion was angiographically normal before the spasm. Spasm was induced in none of 15 pigs before the endothelium was denuded, in five of nine pigs after 1 month, and in five of six pigs after 3 months (Table 1). Significant electrocar-

Table 1. Number of pigs in which coronary artery spasm was induced before and after endothelial denudation of the left circumflex coronary artery and before and after the intracoronary (i.c.) or intravenous (i.v.) administration of various drugs. The doses of each drug were as follows: histamine, i.c. 100 or 400 μg and i.v. 10 or 100 μg/kg; cimetidine, i.v. 60 mg/kg; serotonin, i.c. 60 μg and i.v. 30 μg/kg; phenylephrine, i.c. 20 μg and i.v. 3 μg/kg; ergonovine, i.v. 0.2 or 0.4 mg.

Group	Route of administration	Before denudation	After denudation	
			1 month	3 months
Total		0/15	5/9	5/6
Histamine	i.c.	0/1	1/2	2/2
Histamine	i.c.	0/3	5/6	3/3
Histamine plus cimetidine	i.v.	0/7	2/7	2/4
Serotonin	i.c. or i.v.	0/3	1/4	0/4
Phenylephrine	i.c. or i.v.	0/3	0/4	0/5
Ergonovine	i.v.	0/15	0/8	0/5