

Disentangling defense: the function of spiny lobster sounds

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Summary

The function of anti-predator signalling is a complex, and often-overlooked, area of animal communication. The goal of this study was to examine the behavioural function of an anti-predator acoustic signal in the ocean. We observed the acoustic and defensive behaviours of California spiny lobsters (Palinuridae: *Panulirus interruptus*) to a model predator, model conspecific and blank pole, both in the tank and in the field. We found that *P. interruptus* make a ‘rasp’ sound once physically contacted by an aggressor, rather than during the approach. The model predator and conspecific elicited no discernable changes in defensive behaviour, but the responses by the lobsters to aggressors in the tank versus field were distinct. Our results indicate that the spiny lobster’s rasp is used as a startle or aposematic signal, which may be coupled with visual aposematism of their spines. Alternatively, the rasp may function as a vibratory escape mechanism or as an acoustic analogue to eye-spots. This study offers insights into the role of acoustic signalling in the marine environment and demonstrates a central role for sound production in spiny lobster ecology.

Keywords: anti-predator signals, aposematism, warning, startle, Palinuridae.

Introduction

“As a general rule it is better to mate tomorrow than be a meal today”
(Bailey, 1991).

Approximately 125 million years ago, spiny lobsters evolved a sound-producing apparatus at the base of their spiny antennae (Palero et al., 2009).

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Lacking claws, palinurid lobsters rely on their long and powerful antennae to defend themselves against intruders (Kanciruk, 1980; Spanier & Zimmer-Faust, 1988; Kelly et al., 1999; Herrnkind et al., 2001; Barshaw et al., 2003; Briones-Fourzán et al., 2006). With the origin of the sound-producing apparatus in one group of spiny lobsters (the ‘Stridentes’) (George & Main, 1967), the antennae became both mechanical and acoustic weaponry (Patek & Oakley, 2003). Indeed, since its origin, the sound-producing apparatus has diversified into a fantastic array of sizes, shapes and colors (George & Main, 1967; Patek & Oakley, 2003). Given that the acoustic structures are indistinguishable between males and females (Patek, 2002; Patek & Oakley, 2003; Patek & Baio, 2007; Patek et al., 2009), and that the spiny lobsters produce the sounds when interacting with potential predators, the function of the sound is assumed to deter predators (Lindberg, 1955; Moulton, 1957; Moulton, 1958; Smale, 1974; Meyer-Rochow & Penrose, 1976; Mulligan & Fischer, 1977; Bouwma & Herrnkind, 2009). Remarkably, over the millennia of documentation of these sounds in the literature (Athenaeus, 3rd century; Parker, 1878, 1883), not until recently has the anti-predator function of these signals been experimentally tested (Bouwma & Herrnkind, 2009). Even with this foundational study of function, how the spiny lobsters’ sounds deter predators (Edmunds, 1974; Bradbury & Vehrencamp, 1998; Caro, 2005) remains unknown in this system.

Most spiny lobster taxa exhibit forms of gregarious behaviour that offer defense against predators (Butler IV et al., 1999; Kelly et al., 1999; Herrnkind et al., 2001; Barshaw et al., 2003; Childress, 2007; Briones-Fourzán & Lozano-Álvarez, 2008). For example, many species share dens (Childress & Herrnkind, 1997; Childress & Herrnkind, 2001), aggregate when presented with predators (Kelly et al., 1999; Herrnkind et al., 2001), migrate in formation (Bill & Herrnkind, 1976) and sense conspecific olfactory alarm signals (Shabani et al., 2008). The spiny lobster’s acoustic signal, the ‘rasp’, is used in both solitary and gregarious settings when interacting with potential predators (S.N.P., pers. observ.). Three behavioural studies have suggested the possibility of intraspecific communication with sound as acoustic warning signals to conspecifics (Lindberg, 1955; Berrill, 1976; Meyer-Rochow et al., 1982), but strong experimental evidence is lacking and it is not presently known whether spiny lobsters can hear beyond the near-field region (approx. 1 wavelength from the source = 4 m: Patek et al., 2009) (reviewed in Budelmann, 1992; Popper et al., 2001).

The sound-producing mechanism itself may relate to its anti-predator function. Spiny lobsters produce sound by rubbing a soft-tissue extension (the ‘plectrum’) at the base of each antenna over an oblong, macroscopically smooth ‘file’ under each eye; rasp sounds are generated using stick-slip friction between the two surfaces (Patek, 2001, 2002; Patek & Baio, 2007). Patek (2001) proposed that the use of non-rigid surfaces to produce these stick-slip sounds allowed the animals to generate sound throughout their moult cycles when the exoskeleton is softened, thereby providing an acoustic defence when their other physical defences are compromised. Latha et al. (2005) confirmed that recently moulted lobsters can effectively generate loud rasps.

The first published performance tests of the spiny lobster’s anti-predator rasp examined how silencing Caribbean spiny lobsters (*Panulirus argus*) affected their nocturnal interactions with predatory octopus (*Octopus briareus*) in experimental tanks (Bouwma & Herrnkind, 2009). The authors found that stridulating lobsters were better able to escape octopus attacks and resist attacks for a longer duration than silenced lobsters. While the first approach of the octopus did not yield an acoustic response until physical contact with the lobster, in subsequent approaches, the spiny lobsters initiated tail flip escape responses (not necessarily with sound) before contact. Once caught, the lobsters stridulated for an extended time (average 90 s). Even though the stridulating lobsters fared better than the silenced lobsters, the octopuses showed no obvious response to the rasp signal, leading the authors to suggest that perhaps the rasp does not function to startle the octopus and instead the vibrations make it more difficult to grasp the rasping lobster. While this study offers a number of keen insights into the acoustic function of the rasp, it is important to note that there was no control for the surgery that removed the sound-producing apparatus in silenced lobsters. Given that the plectrum is an integral part of the antennal joint (Patek, 2002), it is possible that the differences in performance could be due to the experimental removal of this joint articulation, rather than the absence of sound production. In an unpublished dissertation (Bouwma, 2006), similar performance results were found in daytime face-offs between triggerfish and tethered silenced and stridulating spiny lobsters.

Ideally, in order to determine the behavioural function of the rasp, one would observe naturally occurring predator–prey interactions in the field with freely-moving individuals (e.g., Cocroft, 1999). However, spiny lobsters pose particular challenges to this experimental approach. First, spiny lobsters are nocturnal foragers, often going on excursions far from their

daytime rocky and coral crevices, thus making visualization of behaviours and tracking difficult. Nonetheless, illumination at night with red lights is minimally disruptive to spiny lobsters, although the lights can attract small fish (Weiss et al., 2006). Second, and more critically, spiny lobsters generate these rasp sounds in water. Sound travels approximately five times more quickly in water than in air, making localization of sounds nearly impossible without an array of hydrophones or only while in very close range of the sound source. Furthermore, the ambient background noise in their habitats can be high enough that rasps may not be reliably recorded from distances beyond approx. 1 m from the source (Patek et al., 2009). Tethering lobsters is one solution, but it affects the ability of the lobsters to escape, and, therefore, the dynamics of the predator–prey interactions and the type of predators that approach (Zimmer-Faust et al., 1994) as well as possibly the acoustic behaviour of the lobsters (Bouwma & Herrnkind, 2009).

Given these limitations, one approach is to conduct the experiments in the field with freely-moving spiny lobsters, record the rasps in close range and use model predators rather than real predators. Numerous studies have documented the importance of olfactory cues during predatory interactions (e.g., Sih et al., 1998; Dicke & Grostal, 2001; Lima, 2002). Clawed lobsters (Nephropidae) (Wahle, 1992) and spiny lobsters (Berger & Butler IV, 2001) are able to detect predators using chemical cues. In addition to chemoreception, crustaceans use their antennae as mechanosensory structures and can detect the low-frequency signatures of locomoting animals (Tautz & Sandeman, 1980; Tautz, 1990; Derby & Steullet, 2001). Thus, models would lack both the olfactory cues of predators and the finer-tuned vibratory cues of swimming predators. However, the models would generate the low-frequency waves produced by any approaching object in a fluid environment, thus giving them advanced warning of an approaching model predator. Visual cues, however, can be sufficient to alert arthropods to predators; in a study of spider responses to a range of predator signals, spiders were able to appropriately respond solely on the basis of visual cues (Lohrey et al., 2009). In addition, the study by Bouwma and Herrnkind (2009) on octopus predators suggest that the visual and physical contact experience may supersede ambient olfactory cues in the Caribbean spiny lobster.

Thus, in this study, we present the first published field and laboratory experiments to examine the behavioural function of rasps produced by freely-moving California spiny lobsters (*Panulirus interruptus*) interacting with a model predator, a model conspecific and a blank pole. *Panulirus interruptus*

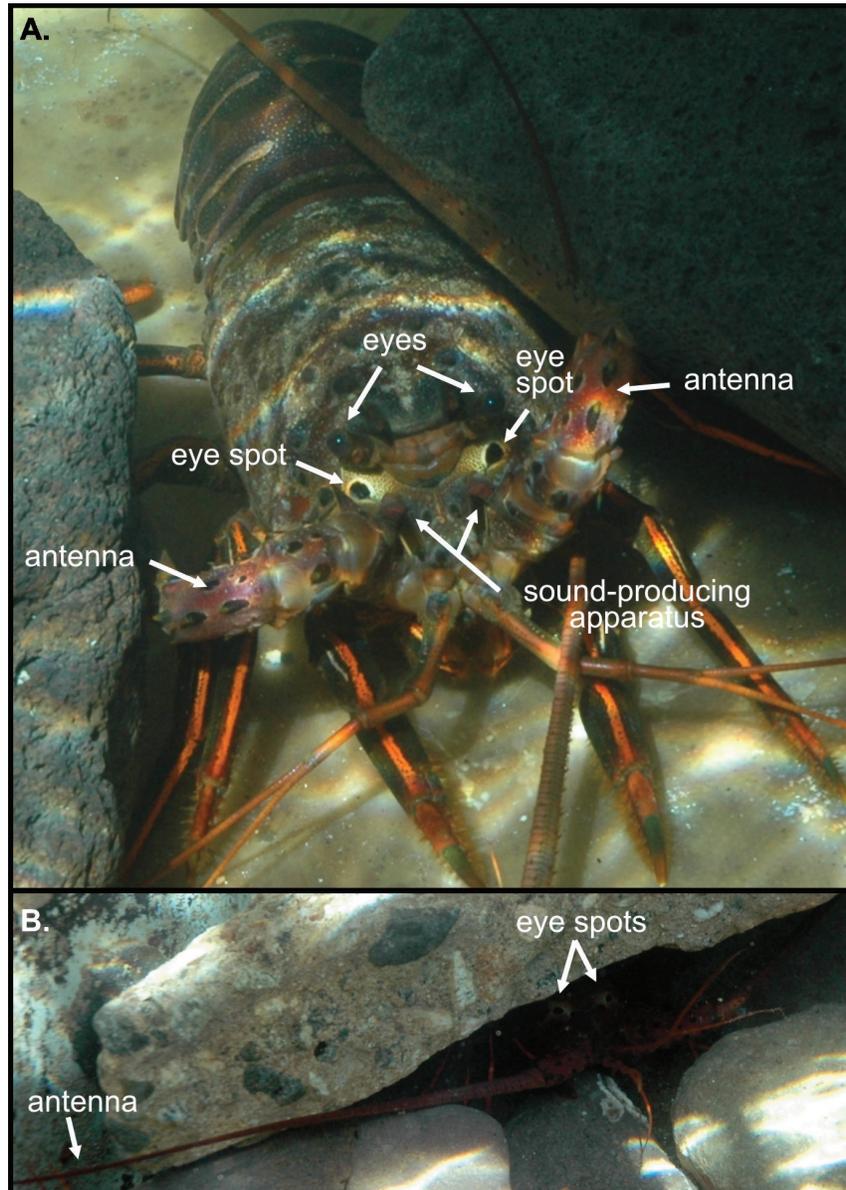


Figure 1. The California spiny lobster (*Panulirus interruptus*) hides in rocky crevices during the day (A) and often the only visible parts of the body are the extended antennae and eye-spots (B). The sound-producing apparatus is located at the base of each antenna, beneath the eyes. The characteristic eye-spots are located adjacent to the sound-producing apparatus, immediately below the eyes. This figure is published in colour in the online version of this journal, which can be accessed via <http://www.brill.nl/beh>

are gregarious (although coordinated anti-predator behaviours have yet been described in this species), nocturnal spiny lobsters with brightly coloured ‘eye-spots’ adjacent to their sound-producing apparatus (Figure 1). Like

other sound-producing spiny lobsters, this species also generates stick-slip ‘rasp’ sounds when interacting with potential predators (Patek & Baio, 2007; Patek et al., 2009). We addressed three central questions. First, based on the timing and context of sound production, which type of anti-predator signal is being used? Second, do spiny lobsters respond differently to a model predator than to a control model (conspecific) or a blank pole? Lastly, given that most previous studies of anti-predator signaling have taken place in the laboratory or confined conditions, how does defensive behaviour vary between field and tank environments?

Materials and methods

Lindberg (1955) found that sheepshead (*Pimelometopon pulchra*) preyed most heavily on *P. interruptus*; thus, one of our models approximated the size and morphology of a sheepshead fish. A second model represented a spiny lobster as a generally non-predatory aggressor. We cast a frozen fish (33 cm body length) and a frozen spiny lobster (8 cm carapace length) with a commercial mold material, and then made the models with a commercial silicone material and spray paint (alginate mold and Silicone RTV SR-1610, Douglas and Sturgess, Richmond, CA, USA). We also used a blank pole (without an attached model) as a control.

During all of the experiments, we simultaneously recorded the lobsters’ behavioural and acoustic responses using two separate audio–video systems, one attached to the aggressor pole and one attached to the observer pole (Figures 2 and 3). By using two systems, we could verify the timing of acoustic response from two vantage points during the experiments. The first system, which we call the ‘aggressor pole’, was used to approach the lobsters with the model aggressor. This pole was equipped with a hydrophone (20–25 000 Hz; HTI-96-Min hydrophone, High Tech, Gulfport, MS, USA), a low-light camera (Submersible Under-Water CCD 480TVL Bullet Color Camera, Sony, New York, NY, USA) and a small, dimmed, white dive light. Depending on the particular experiment, the aggressor pole also had the fish or lobster model attached to it. The second system, termed the ‘observer pole’, recorded the sound of the focal lobster before and during the approach of the aggressor pole. The observer pole was equipped with the same type of hydrophone as the aggressor pole. The video and audio data were recorded

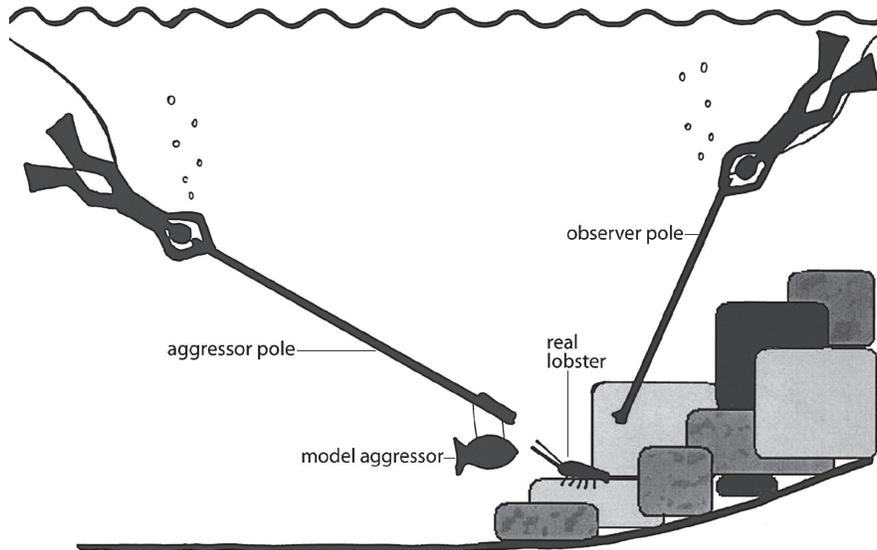


Figure 2. Field experiments were conducted with an aggressor pole and observer pole focused on a freely-moving live spiny lobster. A hydrophone, camera and small flashlight were attached to the aggressor pole. Only a hydrophone was attached to the observer pole. Both poles had cables leading to recording devices on the surface. For each experiment, one person held the observer pole above the lobster, while the other person approached the lobster with the aggressor pole equipped with either a model fish, model lobster, or blank pole.

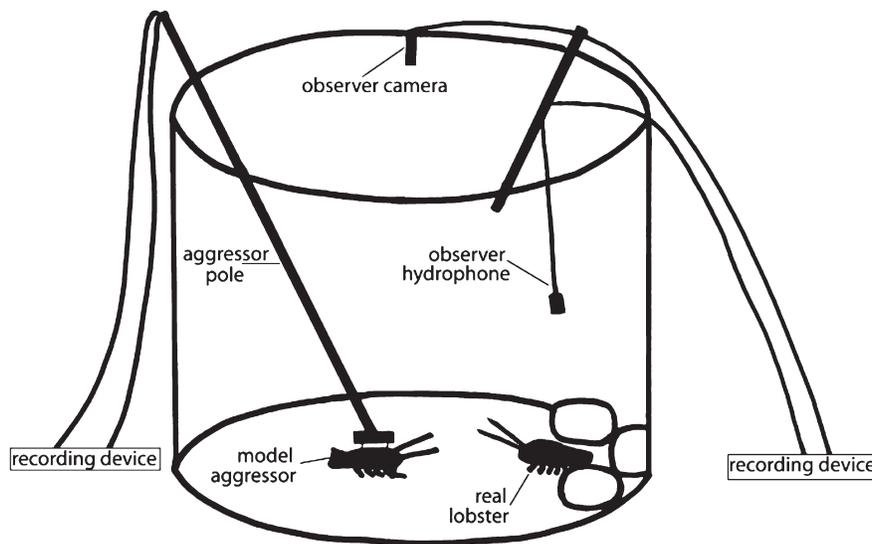


Figure 3. Tank experiments utilized an aggressor and observer pole setup similar to the field experiments. A camera, hydrophone and small dimmed dive-light were attached to the aggressor pole. The observer hydrophone was positioned above the lobster, and the observer camera was positioned at a right-angle to the aggressor pole to capture the lobster's behaviour during the approach. We approached lobsters with the aggressor pole, equipped with either the model fish, model lobster, or a blank pole.

for both poles using the same equipment (Sony GV-A500 Hi8 Video Walkman, Sony; digital audio recorder, 48 kHz sample rate, maximum 20 kHz frequency response (-0.5 dB), PMD670, Marantz, Mahwah, NJ, USA).

Experiment 1: response to nocturnal approaches in the field

The goal of this experiment was to measure the defensive acoustic and behavioural responses of spiny lobsters during nocturnal foraging. Spiny lobsters hide deep in rocky crevices during the day and emerge to forage at night. As a result, they were inaccessible to our equipment during the day and we only conducted experiments at night. During these nocturnal experiments, one person held the observer pole above the lobster while a second person approached the lobster with the aggressor pole (both scientists were equipped with snorkelling equipment). The observer pole was used to record the acoustic response during the approach of the aggressor pole, and after the pole made contact with the lobster (Figure 2).

Data were collected in three distinct regions of the subtidal zone; each region was sampled twice, over a two-month interval in the spring of 2008 (Big Fisherman's Cove, University of Southern California, Wrigley Institute for Environmental Studies, Santa Catalina Island, CA, USA). The data from one region were eliminated from the first sampling session due to technical problems. Water temperature ranged from 16–20°C. We approached different individuals for each trial; however, there are thousands of lobsters living in this marine sanctuary, so there is a small chance that the same lobsters were measured twice across the two-month interval.

Experiment 2: response to nocturnal and diurnal approaches in tanks

In the spring of 2008, spiny lobsters were collected at Santa Catalina Island in baited lobster traps or by hand (CA Department of Fish and Game permit No. SC-5751). The lobsters were maintained in a large rectangular tank with a continuous supply of seawater (14–16°C) and were fed frozen squid every two days. Twenty-eight females (carapace length range: 68–104 mm) and 15 males (carapace length range 64–111 mm) were used for this study. Lobsters were transferred individually to cylindrical experimental tanks (152 cm diameter, 81 cm deep); each tank had a burrow made of rocks. Lobsters were given 15–30 min to acclimate before the trial began. After each trial, we determined the animal's sex and measured its carapace length to the nearest

0.01 mm (Absolute Coolant Proof Digital Calipers IP67, Mitutoyo, Hacienda Heights, CA, USA).

We used the same aggressor pole setup as in the field experiments. The ‘observer pole’ from the field experiments was separated into an ‘observer hydrophone’ and an ‘observer camera’ to capture lobster behaviour from a distance and record the acoustic response before and during the entire trial (Figure 3). We performed tank trials both at night (2200–0400 h) and during the day (0900–1800 h). All tank experiments were performed during the first field session.

Experimental design

As we approached lobsters in both the tank and the field, we presented the fish, lobster, or blank pole at random. In the tank trials, we randomized the aggression level of the aggressor pole, and made physical contact with the lobsters in about half of the trials. In the field, randomization of physical contact was attempted but not always possible due to logistical constraints. For the field experiments, we approached 98 lobsters. For the tank experiments, 14 lobsters were first sampled during the day, then at night, and the other 29 lobsters were sampled first at night, then during the day.

Analysis of lobster behaviour and sound production

In order to independently analyze the acoustic and behavioural responses of the lobsters, we digitally separated the video and audio recordings from each trial (iMovie 4.0.1, Apple, Cupertino, CA, USA; Raven 1.3, Cornell Lab of Ornithology, Ithaca, NY, USA). Audio recordings were scanned visually and acoustically for the stereotypical ‘rasp’ spectrogram (settings: Hanning window, 512 sample window size; 3 dB filter bandwidth at 135 Hz resolution) (Figure 4) and waveform. Each video trial was watched several times and the movements of the lobsters were described and quantified (Table 1). Any trials in which we could not see at least the anterior end of the lobster were omitted from analysis.

χ^2 tests were used to determine whether aggressor type, exposure, or direction of approach relative to antennal position affected lobster behaviour or rasping during the approach (cf. Table 1 for details). We noted whether the lobsters made sound during the approach (before physical contact) or during the attack (once physical contact was made), because this information can be

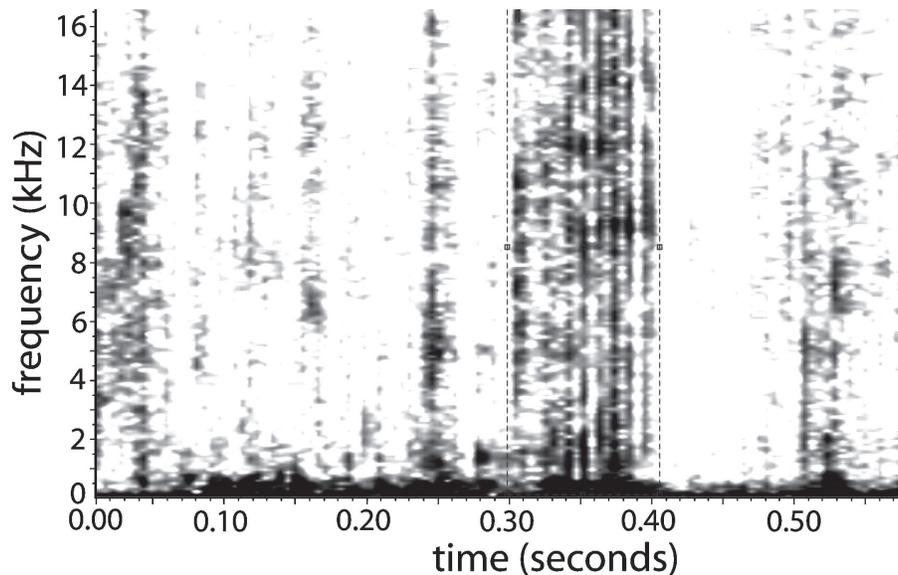


Figure 4. A typical rasp spectrogram from a field recording. One rasp is indicated between the dotted vertical lines. The rasp is composed of a series of broadband pulses.

Table 1. The definitions and states of the variables used in the behavioural analyses.

Variable	Definition
Exposure	Not exposed = lobster hidden in burrow Partially exposed = lobster near shelter (< approx. 1 m) Exposed = lobster distant from any shelter (> approx. 1 m)
Direction of approach relative to antennal position	Match = anterior approach with forward antennae; lateral approach with antennae pointing out; posterior approach with posteriorly-pointing antennae Non-match = anything that is not a match (dorsal approach is always a non-match)
Behavioural response of lobster	Behaviour 1 = no movement of antennae or other body parts Behaviour 2 = movement of antennae/antennules towards camera but minimal leg movement Behaviour 3 = movement of antennae/antennules and use of legs to move away from camera Behaviour 4 = tail flip
Physical contact	Contact = model or pole touches the lobster No contact = nothing touches the lobster
Rasp	Present = lobster makes at least one identifiable rasp Absent = no rasps detected

used to determine which signal type the lobsters are using (see Discussion). We also compared the lobsters' response between the tank and field using the first field session only. To compare the lobsters' rasping and behaviour during the day and at night in the tanks, we performed paired McNemar tests.

Results

Experiment 1: response to nocturnal approaches in the field

The aggressor type, exposure and direction of approach relative to antennal position did not affect lobster behaviour or rasping during the approach (Table 2). We did, however, find a difference in lobster behaviour once the aggressor made physical contact with the lobster ($\chi^2 = 47.1$; $df = 3$; $p < 0.001$). After contact was made, lobsters exhibited a tail-flip escape response 95% of the time (Table 2), whereas when no contact was made,

Table 2. Statistical results of the aggressor experiments across field and tank trials.

Trial	Variable	Behaviour		Rasp	
		df	χ^2	df	χ^2
Field	Aggressor type	6	11.79	2	0.35
	Exposure	6	7.41	2	0.20
	Direction of approach relative to antennal position	3	0.33	1	0.85
	Contact	3	47.05**	1	10.81**
Daytime tank	Aggressor type	6	9.39	2	3.56
	Exposure	6	2.30	2	1.08
	Direction of approach relative to antennal position	3	6.99	1	0.23
	Contact	3	4.17	1	1.97
Nighttime tank	Aggressor type	6	2.89	2	0.05
	Exposure	6	16.35*	2	5.06
	Direction of approach relative to antennal position	3	6.61	1	0
	Contact	3	5.62	1	1.05

Chi-square analyses were used to test the correlation between the behavioural response and aggressor variables, as well as the presence or absence of a rasp in response to the aggressor variables (Table 1). Results are shown as degrees of freedom and chi-square value. * $p < 0.05$, ** $p < 0.01$.

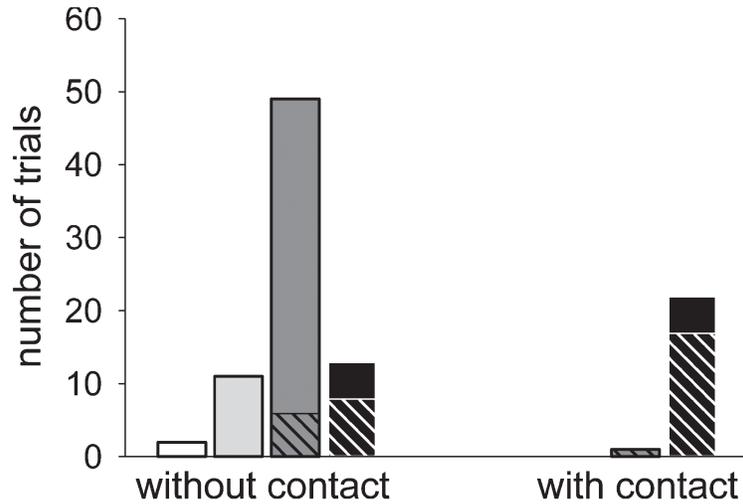


Figure 5. Defensive behaviour of lobsters depending the presence or absence of physical contact with an aggressor. The total number of trials is indicated for each bar; data from the first field session are represented by the hatched portion of the bar and data from the second field session are represented by the solid portion of the bar. While antennal and leg movement (dark grey) and tailflips (black) were observed in both treatments, antennal movement only (light gray) and no movement (white) were only observed in trials with no contact. In both field sessions, more tail-flips occurred after physical contact with an aggressor.

lobsters tail-flipped only 17% of the time (Figure 5). We also observed a difference in lobster rasping depending on contact ($\chi^2 = 10.8$; $df = 2$; $p = 0.001$); lobsters rasped in 56% of the trials when touched, but only rasped in 18% of the trials when not touched (Figure 6).

Given that the two field sessions were conducted over an interval of two months, we independently analyzed the data from each session. In the first session alone, both lobster behaviour ($\chi^2 = 4.414$; $df = 1$; $p = 0.035$) and lobster rasping ($\chi^2 = 3.556$; $df = 1$; $p = 0.059$) were affected by physical contact, although the effect on rasping was not significant (Figures 5 and 6). The second session, however, yielded fewer trials in which we made physical contact with the lobster, which resulted in insufficient data for analysis. Regardless of the aggressor type, exposure, and direction of approach relative to antennal position, we saw a difference in defensive behaviour prior to physical contact between the two field sessions ($\chi^2 = 9.18$; $df = 3$; $p = 0.027$), but there was no difference in the acoustic response prior to physical contact ($\chi^2 = 0.21$; $df = 1$; $p = 0.645$). Lobsters were more physically active in the second field session (when water temperatures were warmer).

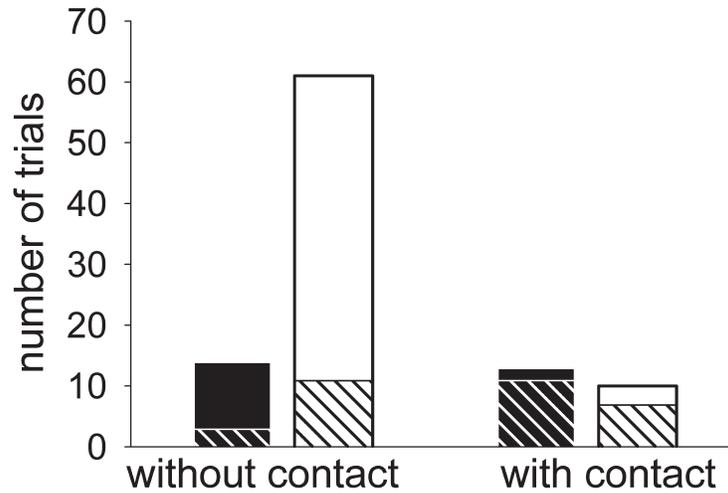


Figure 6. Number of trials with a rasp (black) and without a rasp (white), depending on physical contact by the aggressor (predator, conspecific and blank pole combined). Each bar indicates the total number of trials; within each bar the non-hatched region includes trials from the second field session and the hatched region indicates data from the first field session. There was a significantly higher number of rasps after contact in both experimental datasets.

Experiment 2: response to nocturnal and diurnal approaches in tanks

The aggressor type, exposure (during the day), and direction of approach relative to antennal position had no significant effect on lobster rasping or behaviour during the approach (Table 2). The only significant factor influencing lobster behaviour was the exposure level at night ($\chi^2 = 16.35$; $df = 6$; $p = 0.01$). Exposed lobsters at night were more physically and acoustically active than sheltered lobsters at night or during the day. There was no effect of physical contact on lobster behaviour or rasping in tanks, during the day or at night (Table 2).

Lobsters in tanks responded more actively to intrusion during the day compared to the night (McNemar's test: $\chi^2 = 20.40$, $df = 6$, $p < 0.005$), but their rasping behaviour did not change depending on time of day (McNemar's test: $\chi^2 = 1.5$, $df = 1$, $p = 0.221$). During the day, in 51% of the trials, lobsters pointed their antennae toward the aggressor and retreated more deeply into their shelters. At night, however, lobsters were less active; in 59% of the trials, lobsters did not move their legs or antenna.

Comparison of nocturnal behaviour in the tank versus field

Lobsters exhibited a more physically active behavioural response in the field compared to the tank, both during the approach ($\chi^2 = 31.3$; $df = 3$; $p <$

0.001) and after physical contact ($\chi^2 = 22.1$; $df = 3$; $p < 0.001$). We did not, however, find differences between the acoustic response in the tank versus the field, during the approach ($\chi^2 = 0.14$; $df = 1$; $p = 0.70$) or after contact ($\chi^2 = 2.2$; $df = 1$; $p = 0.14$).

Discussion

Interpreting the function of anti-predator signals is rarely straightforward, given that many are multi-functional, multi-modal and not mutually exclusive. Nonetheless, we can draw conclusions about the function of the spiny lobster's rasp from our experiments, both by using existing frameworks for understanding anti-predator signal function and by examining the use of these signals in the aquatic environment.

Useful for examining the rasp's function, Bradbury & Vehrencamp (1998) offers an organizational framework for the function of what they term 'environmental signals' (Table 3). Environmental signals contain information about external factors, such as available resources or potential predators, and can be directed at either conspecifics or heterospecifics. A starting point for understanding the function of the rasp is to determine whether it is directed at the potential predator or toward conspecifics.

Environmental signals directed toward conspecifics include: (1) recruitment of conspecifics to food resources, (2) low-risk warnings to conspecifics that danger is nearby, possibly including information about the type and location of predator, (3) high risk warnings to conspecifics during attack that put the sender at risk, but the risk is offset by a direct benefit to the sender (Maynard Smith, 1965; Charnov & Krebs, 1975) and (4) distress calls in which conspecifics are recruited to help during attack (Maynard Smith, 1965; Rohwer et al., 1976).

Although not directly related to anti-predator signalling, spiny lobsters regularly recruit conspecifics to feeding sites (a feature used by fishermen who put lobsters in traps to attract more lobsters; Hunt et al., 1986), indicating a gregarious approach to feeding, and, by association, a potential use for gregarious anti-predator behaviours. However, our field observations did not yield any obvious coordinated response to predators – one rasping lobster did not apparently influence nearby lobsters (which typically continued to forage during our simulated attacks), thus suggesting that low-risk warnings are unlikely, although it is possible that the threshold for response was decreased

Table 3. A number of inter- and intra-specific environmental signals are used during interactions with predators (Bradbury & Vehrencamp, 1998).

Signal type	Modality	Sender	Receiver	Timing	Purpose
Inter-specific warning	acoustic	kangaroo rat ¹	snake (predator)	before attack	inform predator that it has been detected
Intra-specific warning	acoustic	squirrel adults ³	squirrel pups	before or during attack	warn offspring of danger
Inter-specific distress	acoustic	starling birds ⁴	raptors (predators)	before or during attack	attract second predator to interfere with first predator's attack
Intra-specific distress	acoustic	marmot pups ²	marmot parents	before or during attack	elicit help from parents
Inter-specific startle	acoustic	insects ⁵	mice, spiders (predators)	during attack	startle predator, induce hesitation
Inter-specific aposematic	acoustic	tiger moths ⁶	bats (predators)	during attack	warn of toxicity
	visual	bivalves, insects, crustaceans ⁷	variety of predators	before or during attack	highlight weaponry (i.e., spines)

Examples of inter- and intra-specific warning, distress, startle and aposematic signals, particularly in the acoustic realm, and their timing relative to predator detection and attack are provided. References: 1, Randall & Stevens (1987); 2, Blumstein et al. (2008); 3, Davis (1984); 4, Hogstedt (1983); 5, Masters (1979); 6, Hristov & Conner (2005); 7, Inbar & Lev-Yadun (2005).

(which we did not assess in this study). Furthermore, there was no indication that the lobsters responded differentially to the predator model and controls and, thus, were unlikely to be providing information about predator type and location to conspecifics. Alternatively, when lobsters congregate in burrows during the day, it is possible that they make use of low-risk warning effects, such as diluting the probability of attack, influencing group movements to decrease success of attack or generating chaos to confuse the predator (Caro, 2005), that we did not observe in these experiments. However, we observed that lobsters in crevices during the day typically retreat further back into the burrow and brace their bodies against the crevice walls rather than chaotically or synchronously swimming out and away.

High risk warnings to conspecifics also seem unlikely given that there are no obvious benefits to helping conspecifics in this system (Maynard Smith, 1965; Rohwer et al., 1976); spiny lobster larvae cycle through the ocean for 6–9 months before settling on the substrate and it is unlikely that co-denning lobsters are kin (Lindberg, 1955; Childress & Hernkind, 1997; Phillips et al., 2006). Lastly, there have been no reports of, and we have never observed, conspecifics offering assistance during attack, making distress signals unlikely. Thus, beyond gregarious feeding, using the rasp as an environmental signal to conspecifics is improbable in this system.

Signals directed toward predators typically (Table 3): (1) warn a predator that the prey is aware of the predator's presence and, thus, is more likely to evade attack (Hasson, 1991; Caro, 1995; Blount et al., 2009), (2) startle the predator, causing the predator to hesitate and providing an opportunity for the prey to escape (Edmunds, 1974; Sargent, 1990; Ruxton et al., 2004), (3) enhance predator learning and avoidance through aposematic signals (e.g., noxious chemicals, abrasive sounds, etc.), such that conspicuous prey are more likely to be avoided (Guilford, 1990; Rowe & Guilford, 1999; Ruxton et al., 2004), (4) inform the predator that a group of animals is cognizant of its presence, typically through mobbing behaviours and (5) attract more predators to generate confusion and perhaps interfere with the initial predator's attack (reviewed in Chivers et al., 1996).

For the interspecific warning function, the spiny lobsters would have to warn the predator in advance of the attack, and we found that lobsters rarely rasped prior to the attack of our model. Physical contact with the model aggressors in our experiment and with the octopus in Bouwma & Herrnkind (2009) was the critical stimulus for generating the rasp. Thus, we can rule out interspecific warning signals as a function for the rasp. The mobbing function is also unlikely, given that most lobster predators are fish that operate in a 3-D environment, whereas lobsters are benthic and lack fine-tuned locomotor control while swimming. Thus, coordinated mobbing behaviour is unlikely and, to our knowledge, has not been observed. More commonly, but something we did not observe with *P. interruptus*, some spiny lobster species aggregate into a circular 'spiny pincushion' to jointly repel predatory attacks (Kelly et al., 1999) rather than aggressively attacking the predator.

The attraction of secondary predators is possible, but also improbable. The rasp is quickly obscured by background noise within 1 m from the source (Patek et al., 2009). Thus, if the rasp were to function in this way,

only nearby predators would be attracted to the scene. That being said, the propagation of olfactory cues is effective and fast in the aquatic environment, and it would seem more parsimonious to expect that the olfactory cues released by damaged tissue would attract secondary predators more quickly and from a greater range. The demonstration of conspecific alarm cues in *P. argus* (Shabani et al., 2008) further suggests that the olfactory channel is an important one during predator interactions.

Thus, using the standard paradigm for anti-predator signal function, the remaining two functions that may be operational in spiny lobster rasps are startle and aposematism. Discerning between a startle and aposematic signal requires several lines of information; it is also important to recognize that these functions are not necessarily mutually exclusive. To demonstrate a startle function, it would be necessary to show that predators pause during attack and that prey subsequently have a higher probability of escape. This would require experiments similar to those conducted by Bouwma & Herrnkind (2009), with the use of a surgical control for silencing the lobsters or an alternative mechanism for silencing that did not require surgery. An aposematic signal requires learning by the predator, such that noxious stimuli (e.g., coloration, noise or odor) increase the learned association with unpalatable prey and, therefore, increase avoidance of the prey (e.g., Rowe & Guilford, 1999; Rowe, 2002; Gamberale-Stille et al., 2009). To test this function in spiny lobsters, it would be necessary to measure the response of initially naïve predators over time as they approach silenced vs. stridulating and palatable vs. unpalatable lobsters.

It is clear from the present study that tank experiments should be approached with caution, whether in the experiments testing the startle or aposematic hypotheses. In the field, lobsters actively foraged away from their dens whereas in the nighttime tank experiments with a short acclimation time, the lobsters hid in their burrows and were minimally responsive to the aggressor. Previous studies of tank-held lobsters suggest that nocturnal foraging resumes after an acclimation period of several hours (S.N.P., pers. observ.), so, at the minimum, future studies should allot more time for the lobsters to re-establish their nocturnal behaviour patterns in a tank.

Anti-predator signaling in air versus water

It is possible that the existing framework for understanding environmental acoustic signals does not fully encompass the realm of signalling in aquatic

environments (e.g., Greenstreet & Tasker, 1996). To our knowledge, there have yet to be any studies of the function and performance of arthropod acoustic anti-predator signals in the aquatic environment. The fundamental difference between terrestrial acoustic signals and aquatic signals is due to the physics of sound and vibration: wavelengths and speed of sound in water are approximately five times greater than in air. As we mentioned above, this leads to difficulties localizing sound sources in water, especially for small animals (Denny, 1993). This also means that animals can sense the vibrational component of sound (the region called the 'near-field'; Kalmijn, 1988) over five-fold greater distances in water than in air and that even animals that lack pressure-sensitive ears can sense most biological acoustic signals within a meter or more of the sound source.

So how might these physical aspects of the aquatic environment affect the range of possible functions for anti-predator signals? The paradigm for acoustic anti-predator signals in the terrestrial environment is that they are broad-band and, therefore, more difficult to localize and not tuned to particular receivers (Morton, 1977). These features are relevant in the ocean as well as in air; however, in water, acoustic signals are inherently difficult to localize, but, more importantly, virtually any receiver could sense a pulsatile signal within 1 wavelength of the source, i.e., in the near-field. Furthermore, beyond one wavelength, the near-field component would be undetectable except to the much narrower range of receivers with pressure-sensitive ears. Given that aquatic crustaceans are not known to have true ears (Budelmann, 1992; Popper et al., 2001) and many lobster predators rely on near-field signals, this close range region offers a highly effective channel for environmental signalling that is absent beyond a few centimetres in the terrestrial environment.

What are the implications of the aquatic environment for the function of the rasp? First, there may not be any need for lobsters to distinguish among predators or other intruders if all can be assumed to sense the rasp. Second, the idea of Bouwma & Herrnkind (2009) that the vibration itself might loosen the predator's grip may be especially relevant in a liquid environment. Indeed, this function might be termed a 'vibratory escape mechanism'. Third, the rasp may function simultaneously as a seismic (through the substrate or body), near-field and far-field pressure-wave signal, whereas in air, the rasp would only be transmitted through the body vibrations and air-borne pressure waves.

Lastly, with sufficient agitation and physical grasping of their antennae, spiny lobsters will automatise one or both antennae (which grow back over subsequent molts). Visually orienting the predator toward the eye-spots that are adjacent to the sound-producing apparatus (Figure 1) and vibrationally orienting a predator toward the extended vibrating antennae may cause the predator to attack the antennae which can be left behind if necessary, thereby allowing the spiny lobsters a costly, but effective escape. In air, a rapidly vibrating antenna would transmit a faint vibrational signal over a millimetre to centimetre length scale which most organisms would be unable to detect. A vibrating antenna in the aquatic environment could generate a vibrational field from centimetres to metres, effective for nearly any aquatic animal's sensory capabilities. Perhaps, in the aquatic environment, such 'acoustic eye spots' may be both more common and effective than presently realized.

Conclusions

Our understanding of anti-predator signals is primarily based upon experimental and theoretical research in terrestrial environments, with research on acoustic anti-predator signals largely conducted on birds and primates (reviewed in Edmunds, 1974; Bailey, 1991; Greenfield, 2002; Ruxton et al., 2004; Caro, 2005). While this research has produced a strong organizational framework for understanding anti-predator signal functions (Edmunds, 1974; Caro, 2005; Bradbury & Vehrencamp, 1998), we are only beginning to understand whether the same principles apply to acoustic signals in the aquatic environment.

An additional consequence of the physics of underwater sound production may be the disproportionate affects of anthropogenic noise on the proper functioning of these systems. For example, anthropogenic noise has decreased the population density (Bayne et al., 2008) and altered acoustic behaviour (Slabbekoorn & den Boer-Visser, 2006) of songbirds. In the marine environment, anthropogenic noise increased the auditory threshold and decreased the ability to detect conspecific signals in fish (Vasconcelos et al., 2007). Marine mammals generated higher amplitude sounds at greater energetic costs to offset high noise levels (Parks et al., 2007; Holt et al., 2009). Studies of noise pollution in the ocean tend to focus on large vertebrates, but the effects of anthropogenic noise on invertebrate communities should also be taken into account when considering the impacts of noise pollution on animal communication systems.

Our study offers some answers to the function of spiny lobster rasps by narrowing the range of possibilities to interspecific startle or aposematic signals while also suggesting future experimental approaches to disentangling the possible signal functions, including what might be termed ‘acoustic eye-spots’ and ‘vibratory escape mechanisms’. In the millions of years since its origin, the spiny lobsters’ acoustic mechanism still poses challenges and offers insights into this untapped frontier of signalling in the sea.

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References

- Athenaeus (3rd century). *Le Banquet des Savants*. — Lamy, Paris.
- Bailey, W.J. (1991). *Acoustic behaviour of insects: an evolutionary perspective*. — Chapman & Hall, New York, NY.
- Barshaw, D.E., Lavalli, K.L. & Spanier, E. (2003). Offense versus defense: responses of three morphological types of lobsters to predation. — *Mar. Ecol. Prog. Ser.* 256: 171-182.
- Bayne, E.M., Habib, L. & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. — *Conserv. Biol.* 22: 1186-1193.
- Berger, D.K. & Butler IV, M.J. (2001). Octopuses influence den selection by juvenile Caribbean spiny lobster. — *Mar. Freshw. Res.* 52: 1049-1053.
- Berrill, M. (1976). Aggressive behaviour of post-puerulus larvae of the western rock lobster *Panulirus longipes* (Milne-Edwards). — *Aust. J. Mar. Freshw. Res.* 27: 83-88.
- Bill, R.G. & Herrnkind, W.F. (1976). Drag reduction by formation movement in spiny lobsters. — *Science* 193: 1146-1148.
- Blount, J.D., Speed, M.P., Ruxton, G.D. & Stephens, P.A. (2009). Warning displays may function as honest signals of toxicity. — *Proc. Roy. Soc. Lond. B: Biol.* 276: 871-877.
- Blumstein, D.T., Richardston, D.T., Cooley, L., Winternitz, J. & Daniel, J.C. (2008). The structure, meaning, and function of yellow-bellied marmot pup screams. — *Anim. Behav.* 76: 1055-1064.
- Bouwma, P.E. (2006). Aspects of antipredation in *Panulirus argus* and *Panulirus guttatus*: behaviour, morphology and ontogeny. — Ph.D. dissertation at Florida State University.
- Bouwma, P.E. & Herrnkind, W.F. (2009). Sound production in Caribbean spiny lobster *Panulirus argus* and its role in escape during predatory attack by *Octopus briareus*. — *N.Z. J. Mar. Freshw. Res.* 43: 3-13.

- Bradbury, J.W. & Vehrencamp, S.L. (1998). Principles of Animal Communication. — Sinauer Associates, Sunderland, MA.
- Briones-Fourzán, P. & Lozano-Álvarez, E. (2008). Coexistence of congeneric spiny lobsters on coral reefs: differences in conspecific aggregation patterns and their potential antipredator benefits. — *Cor. Reefs* 27: 275-287.
- Briones-Fourzán, P., Pérez-Ortiz, M. & Lozano-Álvarez, E. (2006). Defense mechanisms and antipredator behaviour in two sympatric species of spiny lobsters, *Panulirus argus* and *P. guttatus*. — *Mar. Biol.* 149: 227.
- Budelmann, B.U. (1992). Hearing in Crustacea. — In: The evolutionary biology of hearing (Webster, D.B., Fay, R.R. & Popper, A.N., eds). Springer, New York, NY, p. 131-139.
- Butler IV, M.J., MacDiarmid, A.B. & Booth, J.D. (1999). The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. — *Mar. Ecol. Prog. Ser.* 188: 179-191.
- Caro, T. (2005). Antipredator defenses in birds and mammals. — The University of Chicago Press, Chicago, IL.
- Caro, T.M. (1995). Pursuit-deterrence revisited. — *TREE* 10: 500-503.
- Charnov, E.L. & Krebs, J.R. (1975). The evolution of alarm calls: altruism or manipulation? — *Am. Nat.* 109: 107-112.
- Childress, M.J. (2007). Comparative sociobiology of spiny lobsters. — In: Evolutionary ecology of social and sexual systems: crustaceans as model organisms (Duffy, J.E. & Thiel, M., eds). Oxford University Press, New York, NY, p. 272-293.
- Childress, M.J. & Herrnkind, W.F. (1997). Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? — *Mar. Freshw. Res.* 48: 751-758.
- Childress, M.J. & Herrnkind, W.F. (2001). The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. — *Anim. Behav.* 62: 465-472.
- Chivers, D.P., Brown, G.E. & Smith, R.J.F. (1996). The evolution of chemical alarm signals: attracting predators benefits alarm signal senders. — *Am. Nat.* 148: 649-659.
- Cocroft, R.B. (1999). Parent-offspring communication in response to predators in a subsocial treehopper (Hemiptera: Membracidae: *Umberia crassicornis*). — *Ethology* 105: 553-568.
- Davis, L.S. (1984). Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). — *Z. Tierpsychol.* 66: 152-164.
- Denny, M. (1993). Sound in air and water: listening to the environment. — In: Air and water: the biology and physics of life's media. Princeton University Press, Princeton, NJ.
- Derby, C.D. & Steullet, P. (2001). Why do animals have so many receptors? The role of multiple chemosensors in animal perception. — *Biol. Bull.* 200: 211-215.
- Dicke, M. & Grostal, P. (2001). Chemical detection of natural enemies by arthropods: an ecological perspective. — *Annu. Rev. Ecol. Syst.* 32: 1-23.
- Edmunds, M. (1974). Defence in animals: a survey of anti-predator defenses. — Longman Group, Harlow.
- Gamberale-Stille, G., Bragée, C. & Tullberg, B.S. (2009). Higher survival of aposematic prey in close encounters with predators: an experimental study of detection distance. — *Anim. Behav.* 78: 111-116.
- George, R.W. & Main, A.R. (1967). The evolution of spiny lobsters (Palinuridae): a study of evolution in the marine environment. — *Evolution* 21: 803-820.

- Greenfield, M.D. (2002). Signalers and receivers: mechanisms and evolution of arthropod communication. — Oxford University Press, New York, NY.
- Greenstreet, S. & Tasker, M. (1996). Aquatic predators and their prey. — Fishing News Books, London.
- Guilford, T. (1990). The evolution of aposematism. — In: Insect defenses: adaptive mechanisms and strategies of prey and predators (D. Evans & J. Schmidt, eds). State University of New York Press, Albany, NY, p. 23-61.
- Hasson, O. (1991). Pursuit-deterrent signals: communication between prey and predator. — TREE 6: 325-329.
- Herrnkind, W.F., Childress, M.J. & Lavalli, K.L. (2001). Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behaviour. — Mar. Freshw. Res. 52: 1113-1124.
- Hogstedt, G. (1983). Adaptation unto death: function of fear screams. — Am. Nat. 121: 562-570.
- Holt, M.M., Noren, D.P., Veirs, V., Emmons, C. & Veirs, S. (2009). Speaking up: killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. — J. Acoust. Soc. Am. 125: EL27-EL29.
- Hristov, N.I. & Conner, W.E. (2005). Sound strategy: acoustic aposematism in the bat-tiger moth arms race. — Naturwissenschaften 92: 164-169.
- Hunt, J.H., Lyons, W.G. & Kennedy, J.F.S. (1986). Effects of exposure and confinement on spiny lobsters, *Panulirus argus*, used as attractants in the Florida trap fishery. — Fish. Bull. 84: 69-76.
- Inbar, M. & Lev-Yadun, S. (2005). Conspicuousness and aposematic spines in the animal kingdom. — Naturwissenschaften 92: 170-172.
- Kalmijn, A.J. (1988). Hydrodynamic and acoustic field detection. — In: Sensory biology of aquatic animals (Atema, J., Fay, R.R., Popper, A.N. & Tavolga, W.N., eds). Springer, New York, NY, p. 83-130.
- Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). — In: The biology and management of lobsters (Cobb, J.S. & Phillips, B.F., eds). Academic Press, New York, NY, p. 59-96.
- Kelly, S., MacDiarmid, A.B. & Babcock, R.C. (1999). Characteristics of spiny lobster, *Ja-sus edwardsii*, aggregations in exposed reef and sandy areas. — Mar. Freshw. Res. 50: 409-416.
- Latha, G., Senthilvadivu, S., Venkatesan, R. & Rajendran, V. (2005). Sound of shallow and deep water lobsters: measurements, analysis and characterization (L). — J. Acoust. Soc. Am. 117: 2720-2723.
- Lima, S.L. (2002). Putting predators back into behavioural predator-prey interactions. — TREE 17: 70-75.
- Lindberg, R.G. (1955). Growth, population dynamics, and field behaviour in the spiny lobster, *Panulirus interruptus* (Randall). — Univ. Calif. Publ. Zool. 59: 157-248.
- Lohrey, A.K., Clark, D.L., Gordon, S.D. & Uetz, G.W. (2009). Antipredator responses of wolf spiders (Araneae: Lycosidae) to sensory cues representing an avian predator. — Anim. Behav. 77: 813-821.
- Masters, W.M. (1979). Insect disturbance stridulation — its defensive role. — Behav. Ecol. Soc. 5: 187-200.
- Maynard Smith, J. (1965). The evolution of alarm calls. — Am. Nat. 99: 59-63.

- Meyer-Rochow, V.B. & Penrose, J.D. (1976). Sound production by the western rock lobster *Panulirus longipes* (Milne Edwards). — J. Exp. Mar. Biol. Ecol. 23: 191-209.
- Meyer-Rochow, V.B., Penrose, J.D., Oldfield, B.P. & Bailey, W.J. (1982). Phonoresponses in the rock lobster *Panulirus longipes* (Milne Edwards). — Behav. Neur. Biol. 34: 331-336.
- Morton, E.S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. — Am. Nat. 111: 855-869.
- Moulton, J. (1957). Sound production in the spiny lobster *Panulirus argus* (Latreille). — Biol. Bull. 113: 286-295.
- Moulton, J. (1958). Age changes in stridulation and the stridulatory apparatus of the spiny lobsters, *Panulirus argus* (Latreille). — Anat. Rec. 132: 480.
- Mulligan, B.E. & Fischer, R.B. (1977). Sounds and behaviour of the spiny lobster *Panulirus argus*. — Crustaceana 32: 185-199.
- Palero, F., Crandall, K.A., Abelló, P., Macpherson, E. & Pascual, M. (2009). Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). — Mol. Phyl. Evol. 50: 152-162.
- Parker, T.J. (1878). Note on the stridulation organ of *Panulirus vulgaris*. — Proc. Zool. Lond.: 442-444.
- Parker, T.J. (1883). On the structure of the head in *Palinurus* with special reference to the classification of the genus. — Nature 29: 189-190.
- Parks, S.E., Clark, C.W. & Tyack, P.L. (2007). Short- and long-term changes in right whale calling behaviour: the potential effects of noise on acoustic communication. — J. Acoust. Soc. Am. 122: 3725-3731.
- Patek, S. (2002). Squeaking with a sliding joint: mechanics and motor control of sound production in palinurid lobsters. — J. Exp. Biol. 205: 2375-2385.
- Patek, S.N. (2001). Spiny lobsters stick and slip to make sound. — Nature 411: 153-154.
- Patek, S.N. & Baio, J.E. (2007). The acoustic mechanics of stick-slip friction in the California spiny lobster (*Panulirus interruptus*). — J. Exp. Biol. 210: 3538-3546.
- Patek, S.N. & Oakley, T.H. (2003). Comparative tests of evolutionary tradeoffs in a palinurid lobster acoustic system. — Evolution 57: 2082-2100.
- Patek, S.N., Shipp, L.E. & Staaterman, E. (2009). The acoustics and acoustic behaviour of the California spiny lobster (*Panulirus interruptus*). — J. Acoust. Soc. Am. 125: 3434-3443.
- Phillips, B.F., Booth, J.D., Cobb, J.S., Jeffs, A.G. & McWilliam, P. (2006). Larval and postlarval ecology. — In: Lobsters: biology, management, aquaculture and fisheries (Phillips, B.F., ed.). Blackwell, Oxford, p. 231-262.
- Popper, A.N., Salmon, M. & Horch, K.W. (2001). Acoustic detection and communication by decapod crustaceans. — J. Comp. Phys. A 187: 83-89.
- Randall, J.A. & Stevens, C.M. (1987). Footdrumming and other anti-predator responses in the bannertail kangaroo rat (*Dipodomys spectabilis*). — Behav. Ecol. Soc. 20: 187-194.
- Rohwer, S., Fretwell, S.D. & Tuckfield, R.C. (1976). Distress screams as a measure of kinship in birds. — Am. Midl. Nat. 96: 418-430.
- Rowe, C. (2002). Sound improves visual discrimination learning in avian predators. — Proc. Roy. Soc. Lond. B: Biol. 269: 1353-1357.
- Rowe, C. & Guilford, T. (1999). Novelty effects in a multimodal warning signal. — Anim. Behav. 57: 341-346.

- Ruxton, G.D., Sherratt, T.N. & Speed, M.P. (2004). Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. — Oxford University Press, Oxford.
- Sargent, T.D. (1990). Startle as an anti-predator mechanism, with special reference to the underwing moths, (Catocala). — In: Insect defenses: adaptive mechanisms and strategies of prey and predators (Evans, D.L. & Schmidt, J.O., eds). State University of New York Press, Albany, NY, p. 229-249.
- Shabani, S., Kamio, M. & Derby, C.D. (2008). Spiny lobsters detect conspecific blood-borne alarm cues exclusively through olfactory sensilla. — J. Exp. Biol. 211: 2600-2608.
- Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. — TREE 13: 350-355.
- Slabbekoorn, H. & den Boer-Visser, A. (2006). Cities change the songs of birds. — Curr. Biol. 16: 2326-2331.
- Smale, M. (1974). The warning squeak of the Natal rock lobster. — S. Afr. Ass. Mar. Biol. Res. Bull. 11: 17-19.
- Spanier, E. & Zimmer-Faust, R.K. (1988). Some physical properties of shelter that influence den preference in spiny lobsters. — J. Exp. Mar. Biol. Ecol. 121: 137-149.
- Tautz, J. (1990). Coding of mechanical stimuli in crustaceans — what and why? — In: Frontiers in crustacean neurobiology (Wiege, K., Krenz, W.D., Tautz, J., Reichert, H. & Mulloneg, B., eds). Birkhäuser, Basel, p. 200-206.
- Tautz, J. & Sandeman, D.D. (1980). The detection of waterborne vibration by sensory hairs on the chelae of the crayfish. — J. Exp. Biol. 88: 351-356.
- Vasconcelos, R.O., Amorim, M.C.P. & Ladich, F. (2007). Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. — J. Exp. Biol. 210: 2104-2112.
- Wahle, R.A. (1992). Body-size dependent anti-predator mechanisms of the American lobster. — Oikos 65: 52-60.
- Weiss, H.M., Lozano-Álvarez, E., Briones-Fourzán, P. & Negrete-Soto, F. (2006). Using red light with fixed-site video cameras to study the behaviour of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. — Mar. Tech. Soc. J. 40: 86-95.
- Zimmer-Faust, R.K., Fielder, D.R., Heck Jr., K.L., Coen, L.D. & Morgan, S.G. (1994). Effects of tethering on predatory escape by juvenile blue crabs. — Mar. Ecol. Prog. Ser. 111: 299-303.
-