

# Spiny lobsters stick and slip to make sound

These crustaceans can scare off predators even when their usual armour turns soft.

Many arthropods are able to produce pulsed sounds by rubbing a hard pick over stiff macroscopic ridges<sup>1</sup>, rather like dragging a stick over a washboard. Spiny lobsters (Palinuridae) also make pulsed sounds, and here I show that they generate these by virtue of a frictional 'stick-and-slip' mechanism that is more usually associated with bowed stringed instruments. By using this technique rather than a 'hard-washboard' mechanism, lobsters can produce strident warning sounds against predators throughout their moult cycle, including the period when their exoskeleton is softened and they are most susceptible to predation.

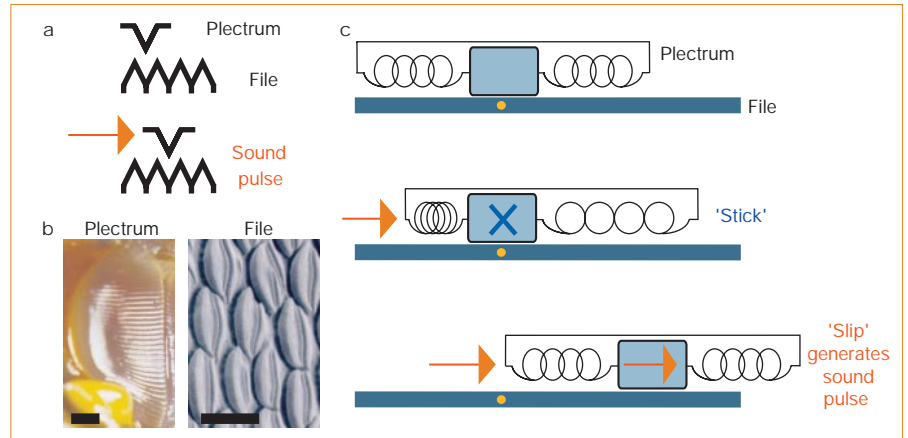
Palinurid lobsters produce a loud, abrasive sound (rasp) by rubbing a plectrum (a basal extension of each antenna) over a file (located on the antennular plate below the eyes; Fig. 1)<sup>2</sup>. This rasp, which is composed of a series of sound pulses, is ostensibly similar to stridulation-based sounds made by crickets, for example, in which a sound pulse is produced when a hard pick (plectrum) hits a macroscopic ridge on the file (Fig. 2a)<sup>1</sup>. However, lobsters produce sound pulses without impact between hard structures; instead, a soft-tissue plectrum rubs over macroscopic shingles on the file (Fig. 2b).

The lobster plectrum and file suggest a frictional mechanism<sup>3</sup> that is analogous to the 'stick-and-slip' that occurs between the bow and string of stringed instruments<sup>4</sup>. In stringed instruments, friction causes the bow to stick momentarily and then to slip relative to the string many times during the course of a single sweep of the bow across the string. This unsteady movement of the bow relative to the string excites vibrations and produces sound. Although theoretically possible in biological systems<sup>5</sup>, such a mechanism has not been found until now.

In the lobster stick-and-slip model,



**Figure 1** 'Face' view of *Panulirus ornatus*, which produces sound using a stick-and-slip mechanism. Eyes are either side of the central orange panel; files are directly below eyes and plectra are the pink structures underneath. Dorsal is towards the top of the page; posterior is into the page.



**Figure 2** Comparison of the 'stick-and-slip' mechanism used by a spiny lobster (*Panulirus argus*) to produce sound and the 'washboard' mechanism typically used by other arthropods. **a**, In typical stridulators such as the cricket, each sound pulse is produced when a hard pick on the plectrum hits a ridge on the file. **b**, Morphology of the sound-production surfaces of the spiny lobster. Soft-tissue plectrum ridges (left) are rubbed posteriorly (to the right as shown) over the anteriorly projecting shingles on the file (right). Scale bars, 500  $\mu\text{m}$  (left) and 15  $\mu\text{m}$  (right). **c**, In the stick-and-slip model, a series of sound pulses is generated when the static friction between the plectrum and file surfaces is periodically exceeded by the sliding friction of the plectrum as it is pulled across the file. Detailed methods are available from the author.

sliding friction between the plectrum and file surfaces would intermittently exceed static friction as the two rub together (Fig. 2c). The soft, elastic tissue of the plectrum resists compression and hence would store energy during the 'sticking' phase and release it during the 'slipping' phase. Each slip between the two surfaces would thus generate a sound pulse.

To test whether palinurid lobsters produce sound using such a stick-and-slip mechanism, I first measured the correlation between plectrum movement and sound production. Using the Caribbean spiny lobster *Panulirus argus*, I attached a motion detector to the plectrum and used a hydrophone to record rasps. Sound was generated only when the plectrum moved posteriorly against the anteriorly projecting shingles on the file. This posterior movement consisted of alternating still and sliding periods; sound pulses were produced only during the sliding movements (97 rasps; 6 lobsters). Using high-speed video analysis, I found that the frequency of shingle impacts was 19,000–28,000 Hz (5 rasps; 1 lobster), which far exceeds the average pulse rate (77 Hz; 139 rasps; 6 lobsters). This is inconsistent with a 'pick-and-washboard' mechanism, in which the pulse rate would be equal to the rate of ridge impact.

A single continuous muscle contraction should be sufficient to produce the series of stepped movements described here, just as a constant driven motion of a bow over a violin string produces repeated sticking and

slipping<sup>4</sup>. Synchronous electromyographic, acoustic and plectrum-movement recordings showed that the promotor muscle<sup>6</sup> contracts tonically during the rasp (120 rasps; 6 lobsters). Thus, a single tonic muscle contraction generates a series of sound pulses. Furthermore, pulsed sound can be generated by manually dragging the plectrum over the file with a single pull. These results are further evidence for the presence of a stick-and-slip mechanism.

When attacked by predators, spiny lobsters produce rasps<sup>3,7,8</sup>, which probably function as a startling deterrent<sup>9</sup>. Lobsters typically rely on their hardened exoskeletons for protection from attack, but they lack such protection when this is softened during the moult cycle<sup>10</sup>. Lobsters do not depend on the hard washboard structures typically used by arthropods to produce sound, but instead make use of frictional interactions between surfaces that do not need to be hard. They can therefore create loud sounds even with a softened exoskeleton during the moult cycle<sup>11</sup>, deterring predators acoustically when their other structural defences are compromised.

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Plant development

## Signals from mature to new leaves

Stomata are microscopic pores on the surfaces of leaves, the number and density of which vary in response to changes in environmental conditions, such as carbon dioxide concentration and light. We show here that mature leaves of *Arabidopsis thaliana* detect and transmit this external information to new leaves of the same plant, producing an appropriate adjustment of stomatal development. As CO<sub>2</sub> concentration controls both stomatal opening<sup>1</sup> and number<sup>2,3</sup>, and stomatal numbers also increase with higher light intensity<sup>4</sup>, the large gradients of CO<sub>2</sub> and light found within plant communities<sup>5</sup> have the potential to influence stomatal development.

Every year, 40% of the CO<sub>2</sub> in the atmosphere passes through stomata<sup>6</sup>. Stomatal numbers modify both photosynthesis and efficient use of water<sup>1</sup>, and so any change in stomatal numbers<sup>7</sup> in response to CO<sub>2</sub> and light can influence photosynthesis and atmospheric CO<sub>2</sub> concentration. The response mechanism described here may exert global effects that are not currently

included in canopy and vegetation models of increasing atmospheric CO<sub>2</sub> levels.

A genetic component in the response of stomatal development to increasing atmospheric CO<sub>2</sub> concentration has been identified<sup>8</sup> and the control of stomatal development by CO<sub>2</sub> concentration is known to occur during early leaf development<sup>9,10</sup>, when ambient CO<sub>2</sub> concentrations may not be accurately detectable by a new leaf sheathed by antecedent leaf primordia<sup>11</sup>. We therefore tested whether CO<sub>2</sub> concentration can be detected by mature leaves in open ambient conditions, which might then transmit a signal to induce an appropriate developmental response by the stomata of new leaves. Our experimental design using the model plant *Arabidopsis thaliana* is shown in Fig. 1a.

Expanding leaves outside the cuvette (ambient CO<sub>2</sub>, 360 p.p.m.), with mature leaves exposed to a high concentration of CO<sub>2</sub> inside the cuvette (720 p.p.m.; Fig. 1a), developed with a reduced stomatal index and density (Fig. 1b, left) compared with control plants grown entirely at ambient CO<sub>2</sub>. Reversing the cuvette arrangement so that the mature leaves were exposed to 360 p.p.m. and the expanding leaves to 720 p.p.m. CO<sub>2</sub> resulted in a complete reversal

(increase) of the stomatal index and density of the new leaves (Fig. 1b, right).

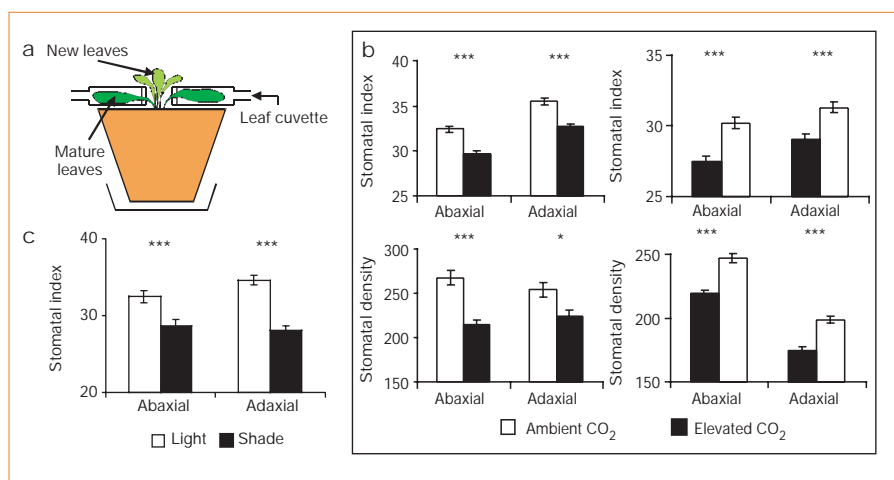
In these experiments, both abaxial (upper) and adaxial (lower) leaf surfaces responded in a similar manner, indicating that CO<sub>2</sub> concentration is detected by mature leaves which signal to expanding leaves to induce an appropriate developmental response. To our knowledge, this is the first demonstration that mature leaves both detect CO<sub>2</sub> concentration and transmit a long-distance signal that controls stomatal development in young leaves. Expanding leaves appeared to have no capacity to detect ambient CO<sub>2</sub> concentration or to respond to it directly by altering stomatal initiation; no cuvette effect was found to contribute to the responses.

This mechanism of CO<sub>2</sub> detection and signalling could enhance or optimize performance in plant communities. For example, the reduction in stomatal index and density with CO<sub>2</sub> enrichment enhances water-use efficiency<sup>3,12</sup>, but such a response will be much less effective<sup>13</sup> when leaves develop in the shade of other plants. We therefore tested whether the mechanisms controlling the response of stomatal initiation to CO<sub>2</sub> might also be accompanied by another that responds to light, reducing the initiation of stomata with increasing shade.

We have previously shown that there is a positive relation in *Arabidopsis* between irradiance and both stomatal index and density. Fully grown leaves were now placed in shaded light, with the expanding leaves under full light. The stomatal index (Fig. 1c) and density (results not shown) of new leaves were reduced, as if they had developed under shade conditions. We conclude that long-distance signalling must also be involved in controlling the response of stomatal development to light, which supports the idea that there is an ecologically important link between the responses evoked by light and by carbon dioxide.

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**Figure 1** Mature leaves detect changes in CO<sub>2</sub> concentration and elicit a stomatal response in developing leaves. **a**, Leaf-cuvette experiment. Plants of *Arabidopsis* (Columbia, Col-0) were grown for 4 weeks under ambient CO<sub>2</sub> (360 p.p.m.) until leaf insertions 5 to 13 had developed. These mature leaves were enclosed in transparent airtight cuvettes under CO<sub>2</sub> concentrations of either 720 or 360 p.p.m. Subsequent leaf insertions developed outside the cuvette under ambient CO<sub>2</sub>. Plants were maintained in cuvettes for 7 to 9 days until the next five leaf insertions had matured, the last three of which were investigated for stomatal density (no. of stomata per mm<sup>2</sup>) and index (no. of stomata/ho. of stomata + no. of epidermal cells) × 100). **b**, (left) Stomatal index and density for new leaves (insertions 16 to 19) under ambient CO<sub>2</sub> when mature leaves (insertions 5 to 13) inside cuvettes are supplied with increased CO<sub>2</sub> (720 p.p.m.). Both stomatal density and index are reduced in new leaves if the supply of CO<sub>2</sub> is increased to the mature leaves. Right, reverse experiment: mature leaves inside cuvettes are under CO<sub>2</sub> at 360 p.p.m.; external CO<sub>2</sub> is 720 p.p.m. Stomatal density and index increase in response to the decreased CO<sub>2</sub> around the mature leaves. **c**, Effect on stomatal index of new leaves of reducing light incident on mature leaves by using neutral density filters (shade) or transparent filters (full light). Stomatal index of new leaves is reduced when mature leaves are shaded. \*\*\*P < 0.0005; \*P < 0.05; bars, s.e.m.; n = 150.

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