

Signaling against the Wind: Modifying Motion-Signal Structure in Response to Increased Noise

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Summary

Animal signals are optimized for particular signaling environments [1–3]. While signaling, senders often choose favorable conditions that ensure reliable detection and transmission [4–8], suggesting that they are sensitive to changes in signal efficacy. Recent evidence has also shown that animals will increase the amplitude or intensity of their acoustic signals at times of increased environmental noise [9–11]. The nature of these adjustments provides important insights into sensory processing. However, only a single piece of correlative evidence for signals defined by movement suggests that visual-signal design depends on ambient motion noise [12]. Here we show experimentally for the first time that animals communicating with movement will adjust their displays when environmental motion noise increases. Surprisingly, under sustained wind conditions, the Australian lizard *Amphibolurus muricatus* changed the structure and increased the duration of its introductory tail flicking, rather than increasing signaling speed. The way these lizards restructure the alerting component of their movement-based aggressive display in the presence of increased motion noise highlights the challenge we face in understanding motion-detection mechanisms under natural operating conditions.

Results and Discussion

The use of movement to communicate is widespread in the animal kingdom, including our own attempts to attract the attention of others by waving our arms and our efforts to enhance this signal in crowded places. In the same way, how well animals can detect rare but important visual motion events is likely to be affected by varying levels of noise in the environment, as has been demonstrated for the acoustic modality [13]. The primary source of motion noise for movement-based signals comes from wind-blown plants (Figure 1A) [14, 15]. Figures 1B and 1C illustrate that the effect of increased wind speed is to generate stronger motion signals; this has been suggested previously [16, 17] but rarely quantified [18]. This figure also demonstrates,

in the case of the aggressive displays of the Jacky lizard (*A. muricatus*), the difficulty faced by the visual system in discriminating a movement-based signal from plant motion on the basis of the overall velocity field. In the present study, we show that lizards do not simply try to generate stronger motion signals to separate their displays from plant motion, but adopt an intermittent-signaling strategy over longer durations that implies a different segmentation mechanism.

The distribution of the Jacky lizard includes large populations along the south-east coast of Australia [19]. These coastal reserves are densely vegetated with compact shrubs that provide protective cover for the substrate from wind exposure [20]. Communication between conspecifics therefore takes place in environments in which variable wind conditions generate irregular patterns of plant motion. We examined whether wind-induced plant motion affected the structure of displays used in territorial disputes by male lizards. We focused on the initial response of residents to potential rivals because this is where reliable detection is paramount for efficient communication. For these lizards, this alerting function is served by a series of tail flicks, which precede a rapid sequence of motor patterns centered on the push up [21]. Attention to the push-up part of the display is crucial because it provides important cues regarding signaler quality to receivers. Male lizards reliably defend territories in captivity [22, 23], and this allowed us to undertake an experiment controlling the environmental conditions at the time of signaling. Such control would be practically impossible to achieve in the natural habitat of the lizards. We allowed the lizards to settle for between 10 and 20 days within large outdoor enclosures featuring branches for basking and plant species consistent with those occurring in the animals' natural habitat (Figure 1A) before revealing a conspecific male intruder from a hide located at the front of the enclosure. Our aim was to compare introductory tail flicking under calm conditions that reflect prevailing winds with that under windy conditions that we controlled with high-speed fans. The enclosures we constructed did not allow us to determine whether lizards modify their signal choreography because they sense the wind directly or because they detect the associated increase in plant motion. Although such a distinction is interesting, for the current study we aimed to mimic as closely as possible the lizards' natural habitat, where they are surrounded by plants, which they rely on for cover from predators.

We found that in windy conditions, Jacky lizards significantly increased the period of time over which they performed the introductory tail flicking before commencing the rest of the display (Figure 2A and Movie S1 in the Supplemental Data available online; $F_{1,8} = 32.09$, $p = 0.0005$). Indeed, longer tail flicking in windy conditions was observed in all lizards (Figure 2B), the tail flicking being 1.6 to 97 times longer than that in calm conditions. Furthermore, the introductory

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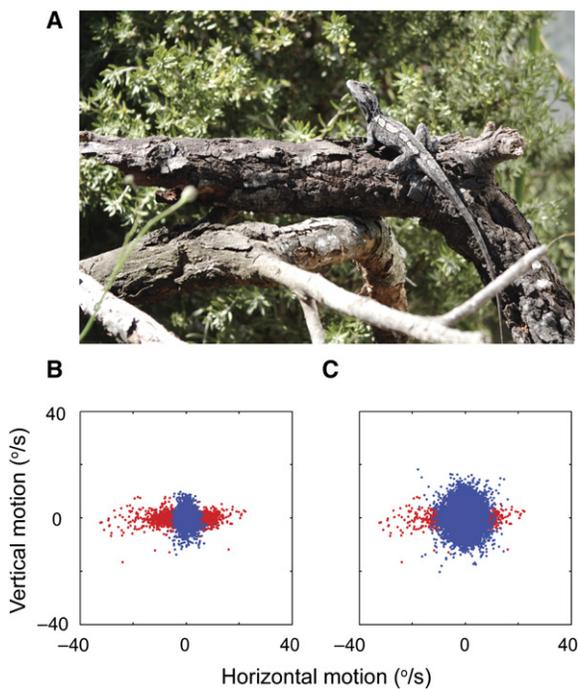


Figure 1. Image Motion Due to Plants Increases in Strength with Stronger Winds

Amphibolurus muricatus display against a background of wind-blown plants (A). The motion of both types of movement can be quantified with motion-detection algorithms, resulting in estimates of image velocity [31]. We analyzed the image motion generated by plants in different wind conditions and summarize here the distribution of motion estimates for *Lomandra longifolia* in calm and windy conditions (0.6–1.2 m/s and 3.5–4.9 m/s wind speed, respectively, recorded 1 m above the ground) and a representative *A. muricatus* display filmed in the absence of background motion. Measured velocity is converted from pixels per frame to °/s on the basis of a viewing distance of 1 m. Eight-second samples for plant motion (blue dots) in calm (B) and windy (C) conditions are overlaid onto those generated by the lizard display (red dots). The effect of increased wind speed on *L. longifolia* is to generate faster motion, as shown by the greater spread of blue dots from calm to windy conditions. The lizard display is likely to be conspicuous in calm conditions (B); however, it would be more difficult to detect in windy conditions (C). Interestingly, the results of the present study show that lizards do not seek to increase the speed of their display to overcome increased motion noise.

component was not characterized by continuous tail flicking in windy conditions. Lizards typically flicked their tails in a continuous fashion in calm conditions, but switched to intermittent flicking during the windy condition (Figure 3A). This difference can be quantified with a measure of signal intensity. Here we define intensity to be the ratio of time spent in motion over total display duration. There is a clear reduction in signaling intensity under windy conditions (Figure 2C; $F_{1,8} = 14.18$, $p = 0.006$), and this in part offsets the overall longer signaling duration under windy conditions. However, despite the intermittency of signaling, the time spent in motion is still longer in windy conditions ($F_{1,6} = 8.11$, $p = 0.029$). Interestingly, though, there was a trend for the time spent in motion to increase with time of day for the windy but not for the calm condition (Figure 2D; interaction term: $F_{1,6} = 5.09$, $p = 0.0649$). Because all fans were started at the beginning of the day, regardless

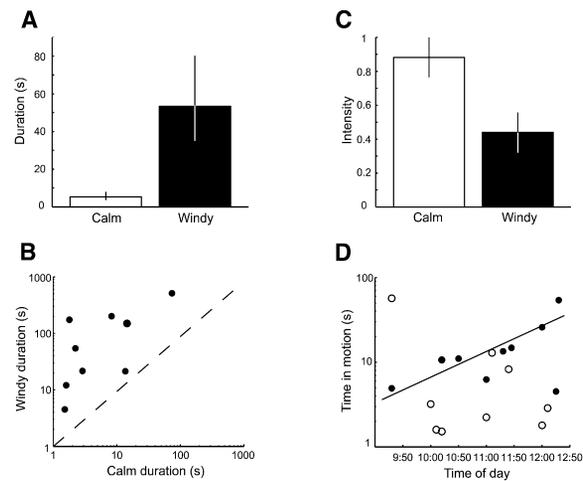


Figure 2. Tail Flicking in Calm and Windy Conditions

(A) Introductory tail flicking by the lizard *A. muricatus* was significantly longer in windy relative to calm conditions ($F_{1,8} = 32.09$, $p = 0.0005$). (B) Longer durations (1.6 to 97 times longer) were recorded for all lizards (circles). (C) To offset the increased duration of signaling, lizards inserted pauses between bouts of flicking, thereby decreasing the intensity of the signal ($F_{1,8} = 14.18$, $p = 0.006$). (D) The amount of time in which the tail was moving as a function of time of day for calm (open circles) and windy (closed circles) conditions. Lizards showed a trend for increased time in motion over the morning during the windy condition but not during calm conditions (black solid line: $F_{1,6} = 5.09$, $p = 0.0649$). This trend can be attributed to the length of time each lizard was exposed to wind prior to signaling. Values shown in (A) and (C) are means and standard errors calculated on a log scale.

of when each lizard was tested, fan duration was strongly correlated with time of day ($r = 0.801$, $t_7 = 3.54$, $p = 0.009$). The fact that time in motion did not change with time of day under calm conditions suggests that lizards increase actual time in motion with increasing periods of strong wind. Although this result only approached significance, it further highlights the lizards' response to varying environmental conditions. Importantly, time of day alone did not influence tail-in-motion time ($F_{1,6} = 0.04$, $p = 0.842$).

These results represent the first experimental evidence for movement-based signal modification due to environmental conditions in any taxonomic group. Importantly, our results also show that this modification of the signal's structure is not receiver driven, but that the signaler responds to the environmental conditions directly. In order to exclude the possibility that the display was modified simply because of a lack of receiver response, we analyzed the opening section of the tail-flick component in more detail. We reasoned that if the lizards simply tail-flicked until they received feedback from the receiver, the modification should develop over time, and that the initial signaling segments should not differ between windy and calm conditions. We therefore compared the introductory component in the calm condition with the lizards' signaling behavior during exactly the same amount of time at the start of signaling during windy conditions (Figures 3A and 3B). We found a significant reduction in signaling intensity in windy conditions ($F_{1,7} = 28.92$, $p = 0.001$). We then considered variation in motion speed by tracking the tip of the tail

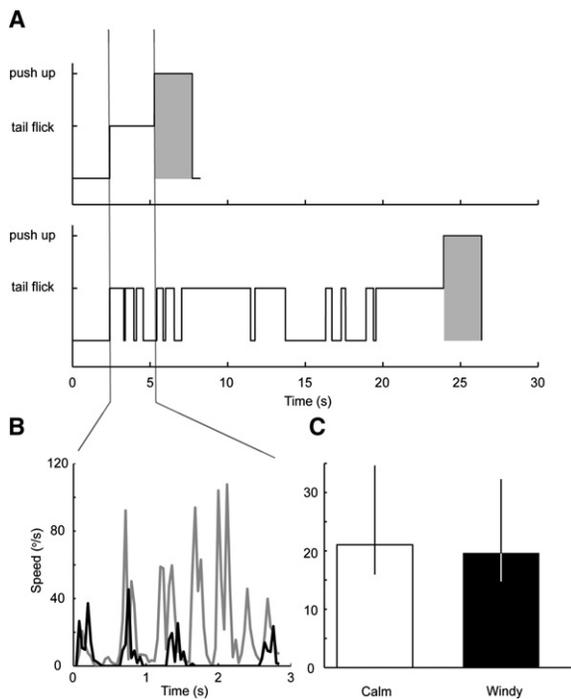


Figure 3. Reduced-Intensity Tail Flicking in Windy Conditions
(A) Time lines depicting the intensity of introductory tail flicking prior to the start of the rest of the display (push up is shaded) for a single male lizard. The top profile depicts continuous tail flicking for about 3 s during calm conditions. The same lizard flicked intermittently for about 21 s during windy conditions, as depicted in the bottom profile. (B) Angular speed was determined for tail flicks in calm conditions (gray line) and the start of the windy condition for the same period (black line). (C) After excluding all zero values reflecting periods when the tail was stationary, the average tail speed does not differ between calm and windy conditions ($F_{1,6} = 0.11$, $p = 0.751$). Values shown are means and standard errors calculated on a log scale.

frame by frame in each sequence (Figure 3B). After pauses were excluded (see Figure 3B), the average angular speed of tail motion did not differ between calm and windy conditions (Figure 3C; $F_{1,7} = 0.11$, $p = 0.751$), suggesting that tail-flick speeds per se do not differ. The lizards thus adopt a strategy of reduced signaling intensity right from the beginning of a display rather than modifying their display because of lack of feedback from the receiver, implying that signaling lizards are sensitive to environmental conditions affecting the efficacy of their signals.

In another lizard species, the detection of oscillating lures against a moving background is facilitated when the lure oscillates at higher frequencies [14], suggesting that these lizards might overcome increased motion noise by signaling at faster speeds (Figure 1) [12]. This is not, however, the strategy adopted by Jacky lizards. In contrast, these lizards favor longer-duration signaling without changing speed. Importantly, the specific adjustments the lizards make to signal production neatly match detection experiments that revealed no efficacy advantage for faster speeds, but significant advantages for longer repetition signaling, and no reduction in efficacy due to reduced intensity [24]. It is likely that the particular pattern of background motion in Jacky lizard

habitats has selected for an alternative strategy to faster signaling. There have been few attempts to characterize plant motion in relation to motion signaling. Using Fourier analysis, Fleishman [25] showed that plant movement had less power at high frequencies than did displays of the lizard *Anolis aeneus*, and this was consistent with the finding that greater display speeds improve the probability of response [14]. We anticipate, therefore, that the signal modifications described herein will be better understood after the achievement of a detailed understanding of the variation in plant motion in calm and windy conditions. That signals are modified at all suggests sensory mechanisms have influenced signal structure in some way. The specific modifications observed in our study provide important starting points for identifying the segmentation mechanisms. We suggest that the spatiotemporal properties of tail flicking overlap with those of wind-blown plants in strong wind conditions. Because wind conditions are extremely variable, however, the masking effect of plant motion will also vary. Increasing the overall display duration, therefore, might improve the chance of the occurrence of tail flicks during lulls in wind conditions, whereby adaptation to background motion [26] is likely to enhance the separation of the two types of motion signals. Furthermore, because the responses of motion-sensitive neurons are characterized by large onset transients [27], a strategy of intermittent signaling generates conspicuous peaks in the input stream to the motion-vision system, representing salient information. The segmentation process we suggest here opens up the intriguing possibility that lizards time their flicks for lulls in wind conditions or for instances of particular motion patterns. Our results thus provide the first direct evidence that environmental conditions at the time of signaling influence movement-based signal design [28]. Furthermore, the specific strategy adopted by these lizards is indicative of an attempt to engage particular properties of the receivers' motion-processing system.

Experimental Procedures

Housing and Apparatus

We constructed four outdoor enclosures (240 × 180 × 90 cm) made from galvanized metal sheets. Each enclosure was set up in the same way with branches for perches raised 40 cm from the ground and located 90 cm from the back and each side. The enclosures were planted with native species typical of the local habitat where these lizards were collected and featured *Westringia fruticosa* (coastal rosemary) as the background to the perches and *Lomandra longifolia* (spiny-headed mat rush) planted along the sides of the pens. A 15 cm square window was cut into the front panel to allow for the filming of lizard responses. A small hide (60 × 45 × 60 cm) constructed from timber and black cloth was erected below the viewing window. The cloth forming the front of the hide was attached to a small dowel stick that could be lowered from outside the enclosure with a fishing line. A plastic aquarium was placed in the hide to house the simulated "intruder". We used a single 40 cm electric floor fan (Dimplex HV46C) for each enclosure to generate constant wind conditions of ~2.5 m/s measured at the midpoint of the perch. The fan in each enclosure was raised 40 cm above the ground at the edge of one side of the enclosure and in line with the perch. Fans were present in the enclosure for both experimental conditions.

Procedure

Lizards were wild caught from Murrumbidgee National Park, New South Wales (NSW), and housed individually in pens similar to the

testing arenas described above. After a minimum of 3 weeks (up to 8 weeks) in captivity, they were transferred to the testing arena. We tested 16 lizards in blocks of four from November 2006 to January 2007. Half of the lizards experienced calm conditions first and then windy conditions on the following day; the remaining lizards experienced windy conditions first. All testing was conducted between 09:00 and 13:00 hr and on clear, sunny days when natural wind conditions were low and sporadic, and temperatures ranged from 20°C–26°C. At the start of the day, conspecific male intruders were placed in each of the small aquariums, and fans located in pens experiencing windy conditions were turned on. After a minimum of 60 min from when the fans were switched on (range 60–180 min), we revealed the intruder by lowering the front cloth. Filming continued until the “resident” lizard stopped displaying, approached the intruder, or sought cover in the plants. This procedure was repeated on the following day with a different intruder and the other wind condition. Lizards were released at the site of capture by the end of March 2007. The Australian National University’s Animal Experimentation Ethics Committee and the National Parks and Wildlife Service of New South Wales approved all housing and experimental procedures.

Analysis

We restricted our analyses to nine lizards that performed territorial displays in both calm and windy conditions. The excluded lizards either did not perform territorial displays on the first ($n = 3$) or second ($n = 2$) day of testing or performed submissive displays on the first day ($n = 2$). We used an event recorder program (J-Watcher Video [29]) to log behavioral states and to calculate durations with a 40 ms accuracy (PAL frame rate), before statistical analysis was undertaken in R 2.3.1 [30]. All durations were \log_{10} transformed prior to analysis. We set up linear mixed-effects models (LME, R 2.3.1 [30]) fitting wind condition and time of day as fixed factors, and including lizard identity and block number as random factors. In all but one instance, time of day did not predict the outcome, and the models were refitted with this factor excluded. The statistical significance of individual model parameters was tested with the F test. Models were checked graphically for outliers and appropriate error distributions.

Supplemental Data

One movie is available at <http://www.current-biology.com/cgi/content/full/17/14/1231/DC1/>.

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