Leaping eels electrify threats, supporting Humboldt's account of a battle with horses

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In March 1800, Alexander von Humboldt observed the extraordinary spectacle of native fisherman collecting electric eels (*Electrophorus electricus*) by "fishing with horses" [von Humboldt A (1807) *Ann Phys* 25:34–43]. The strategy was to herd horses into a pool containing electric eels, provoking the eels to attack by pressing themselves against the horses while discharging. Once the eels were exhausted, they could be safely collected. This legendary tale of South American adventures helped propel Humboldt to fame and has been recounted and illustrated in many publications, but subsequent investigators have been skeptical, and no similar eel behavior has been reported in more than 200 years. Here I report a defensive eel behavior that supports Humboldt's account. The behavior consists of an approach and leap out of the water during which the eel presses its chin against a threatening conductor while discharging high-voltage volleys. The effect is to short-circuit the electric organ through the threat, with increasing power diverted to the threat as the eel attains greater height during the leap. Measurement of voltages and current during the behavior, and assessment of the equivalent circuit, reveal the effectiveness of the behavior and the basis for its natural selection.

evolution | behavior | Humboldt | electroreception | neuroethology

In 1807, Alexander von Humboldt published his account of a battle between electric eels and horses (1). The stage for this event was set when Humboldt hired local fishermen to supply him with eels for research. Their method was to "fish with horses" (1). About 30 horses and mules were herded into a pool containing eels, which (according to Humboldt) emerged from the mud, swam to the surface, and attacked by pressing themselves against the horses while discharging. The fishermen kept the horses from escaping by surrounding the pool and climbing nearby trees with overhanging branches while crying out and waving reeds. Two horses drowned, and others stumbled from the pool and collapsed. Humboldt thought more horses would be killed, but the eels were exhausted before this happened. Five eels were then captured and Humboldt was able to conduct his experiments (2).

This famous story has been illustrated and recounted many times (3–10) (Fig. 1*A*). However, some have doubted its accuracy (see ref. 8). Sachs (5) suggested the story was "poetically transfigured," Coates (11) flatly considered it "tommyrot," and Moller (8) [and Catania (12)] gently suggested Humboldt's accounts were "tales." The aggressive behavior of the eels, taking the offensive against horses, seems the most fantastic and questionable part of the story. Why would electric eels do this? No similar behavior has been reported since Humboldt's (1) publication.

Here I report that electric eels attack large, moving, partially submerged conductors by leaping from the water while pressing themselves against the threat and discharging high-voltage volleys (Fig. 1*B*). This behavior appears to be ubiquitous for comparatively large eels (over 60 cm). Measurement of the voltage and current delivered to stimuli during this behavior suggest it is a formidable defensive strategy. It allows eels to deliver much of their prodigious electrical power, normally distributed throughout the surrounding water, directly to a threat. Eel responses to simulated predators demonstrate the effectiveness of the behavior for electrifying partially submerged targets. Results are discussed in the context of the eel's habitat, power output, and ability to electrify targets in various configurations.

Results

The behavior described in this investigation was serendipitously discovered during research into electric eel predatory behavior and sensory abilities (12–15). For these previous investigations, eels were transferred from a home cage to an experimental chamber with a net that had a metallic rim and handle. From the outset, eels regularly transitioned from a retreat to an explosive attack when the net approached. They swam rapidly toward the net, followed the metal rim to the point of exit from the water, and leaped upward along the rim and handle, keeping their chin in contact while discharging high-voltage volleys. This behavior was both literally and figuratively shocking (Movie S1). Under no other circumstances were eels observed to leap out of the water.

Fig. 2 provides a schematic illustration of the resulting relative current paths that would presumably exist for different phases of the eel's behavior. To assess the validity of this interpretation, a split conductive rod, or alternatively a split aluminum plate, was used to measure voltage (Fig. 3). One short segment of the rod (Fig. 3 *C* and *D*) or plate (Fig. 3 *E* and *F*) was placed into the water, and the other, longer, segment protruded above the water, with a plastic insulating segment between them. Voltage was measured between the top and bottom segments of the conductors as the eels ascended during their shocking leaps. Fig. 3*B* shows an equivalent circuit. When fully submerged, the resistances include the eel's internal resistance (Ri) and the water resistance (Rw1). As the eel ascends, a new and progressively higher resistance path (Rw2) from the eel's head to the water presumably develops.

The voltage drop across this resistance was measured in the experiments illustrated in Fig. 3 (Movies S2–S5). When considering the results, it is important to note that eels do not modulate the amplitude of their high-voltage output during a volley. Volleys consist of a series of roughly 1-ms duration, monophasic,

Significance

Electric eels are shown to leap from the water to directly electrify threats. This shocking behavior likely allows electric eels to defend themselves during the Amazonian dry season, when they may be found in small pools and in danger of predation. The results support Alexander von Humboldt's story of electric eels attacking horses that had been herded into a muddy pool during the dry season in 1800. The finding highlights sophisticated behaviors that have evolved in concert with the eel's powerful electrical organs.

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Fig. 1. Fishing with horses. (*A*) This illustration depicts the battle between eels and horses observed by Alexander von Humboldt in March 1800. It was published in 1843 as the frontispiece for *The Naturalist Library, Ichthyology, Volume V, Part II, the Fishes of Guiana*, authored by Robert H. Schomburgk, a friend and protégé of Humboldt's (3). (*B*) Example of an eel leaping from the water to shock a simulated predator. LEDs are powered by the eel through a conductive carbon strip taped to the front of the plastic prop. See Movie S8.

head-positive pulses. All three of the eel's electric organs participate in the high-voltage output, and there is no mechanism for eels to increase the total power during a volley (16, 17).

As predicted from the circuit shown in Fig. 3*B*, the recorded voltage increased dramatically as the eels ascended. This effect of increasing voltage in proportion to increasing height of eel leap during the volley was measured in each of three eels (n = 10 trials for eel A and n = 5 trials for eels B and C). The same effect was observed for a fourth eel (eel D) based on eel-powered light-emitting diode (LED) intensity (see Movies S7 and S8). Two additional eels (over 60 cm in length) exhibited the behavior in the course of previous investigations, but no measurements were taken.

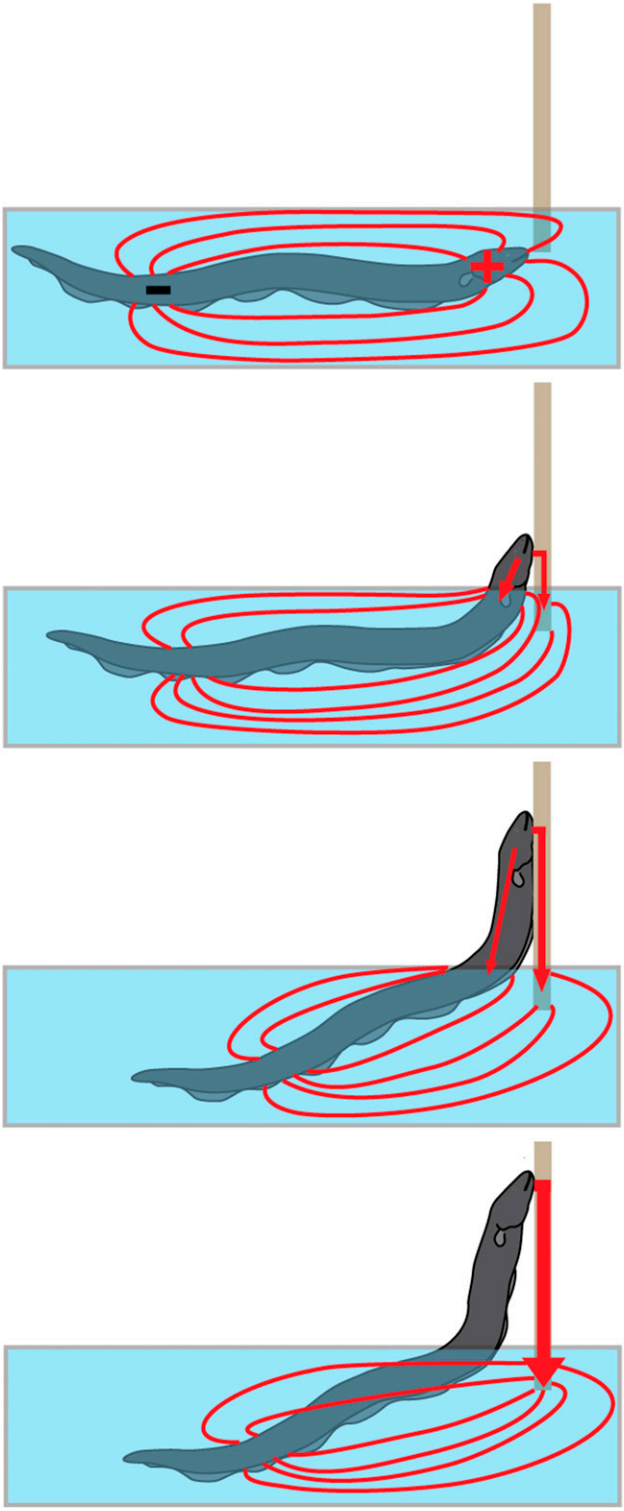

Fig. 2. Schematic of changes to the current path presumed to occur as an electric eel approaches and ascends a conductor. As the eel emerges from the water, two parallel current paths and corresponding resistances exist, representing a current divider. The eel's high voltage is delivered in volleys of roughly 1-ms pulses, and eels do not modulate their total power output during a volley (see text).

The high potential developed between the head and water should reflect a prominent current path if a conductor were present in place of the voltmeter. To directly measure the current flow between the head and water during this behavior, the top and bottom segments of the conductive plate arrangement were directly connected with wires. The current through the wires was measured with a Hall effect sensor that was independent of the circuit (Fig. 4*A* and Movie S6). As predicted, the magnitude of the measured current for each pulse increased dramatically as the eels ascended (five trials each, eels A and C), paralleling the results for voltage (Fig. 4*B*). Fig. 4*C* shows the summed results for voltage and current versus height of leap for eels A and C.

Several features of the leaping behavior suggest it has been selected to maximally electrify terrestrial, or perhaps semi-aquatic, animals. For example, the attack is directed at a novel, moving conductor emerging from the water. In the slow-motion video, the eels can be seen bending their necks to keep their chin in contact with the conductor during the leap. Finally, in some trials, the high-voltage pulse rate was modulated in relationship to conductor contact. See, for example, Fig. 3 *C* and *F* (Movies S2 and S5), showing that the pulse rate rapidly declined to zero once contact was lost, but a new volley was initiated when contact was regained. Thus, the eels are not arbitrarily shocking while they leap; rather, the shocks appear to be directed specifically toward the conductor, based on both body movements and electric organ discharge (EOD) frequency.

In addition to increasing the electrical power delivered to a target, an additional benefit from leaping is the progressive electrification of greater portions of a threatening animal's body that is only partially submerged. To illustrate this effect, sets of eel-powered LEDs were connected in series along separate strips of conductive tape attached, in turn, to a prosthetic limb, allowing direct observation of the increasing area of effect (Movie S7). An additional benefit from the leaping strategy might be gained for targets that have only a small portion of their body submerged but are grounded (5, 18). Eel-powered LEDs were similarly used to illustrate this effect (Fig. 1*B* and Movie S8).

Discussion

The results show that electric eels often respond to a large, moving, and partially submerged conductor with a rapid approach, contact, and then leap up the conductor, keeping the chin in contact while discharging high-voltage volleys. Ascending the conductor progressively increases the resistance of the normal current path from head to tail through the water, replacing it with a new path through the conductive target. The efficacy of this behavior as a defensive strategy seems obvious, but many questions remain. For example, why would electric eels take the offensive, rather than retreating from a potential threat? Why would not hundreds of volts delivered to the surrounding water be a sufficient defense, without the need for a directed attack? What is the likely effect of this behavior on a potential predator? How might the behavior have evolved? Finally, what do these findings suggest about Humboldt's account from 1800 (1)?

Electric eels most likely use an aggressive attack to defend themselves because they often cannot retreat. Amazonia and nearby areas are subject to huge variations in seasonal rainfall that produce a rainy season and a dry season, with major effects on fish communities (19–26). During the rainy season, vast areas of forest and savannah are inundated with water, and dry or low streams and rivers are filled, often rising by several meters. These flooded areas are populated by myriad species of fish, including electric eels (27, 28). When the water rapidly recedes in the dry season, many isolated pools, water-filled holes, and oxbows remain, containing large assemblages of fish. These fish are trapped, either by design or circumstance, until the next rainy season. Electric eels are obligate air breathers (29), well-suited to survive in, and perhaps specialized for (30, 31), these isolated areas that often become deoxygenated (31). The yearly rainfall cycle is well known to native fishermen and investigators of South American fish, and both groups take advantage of the dry season for

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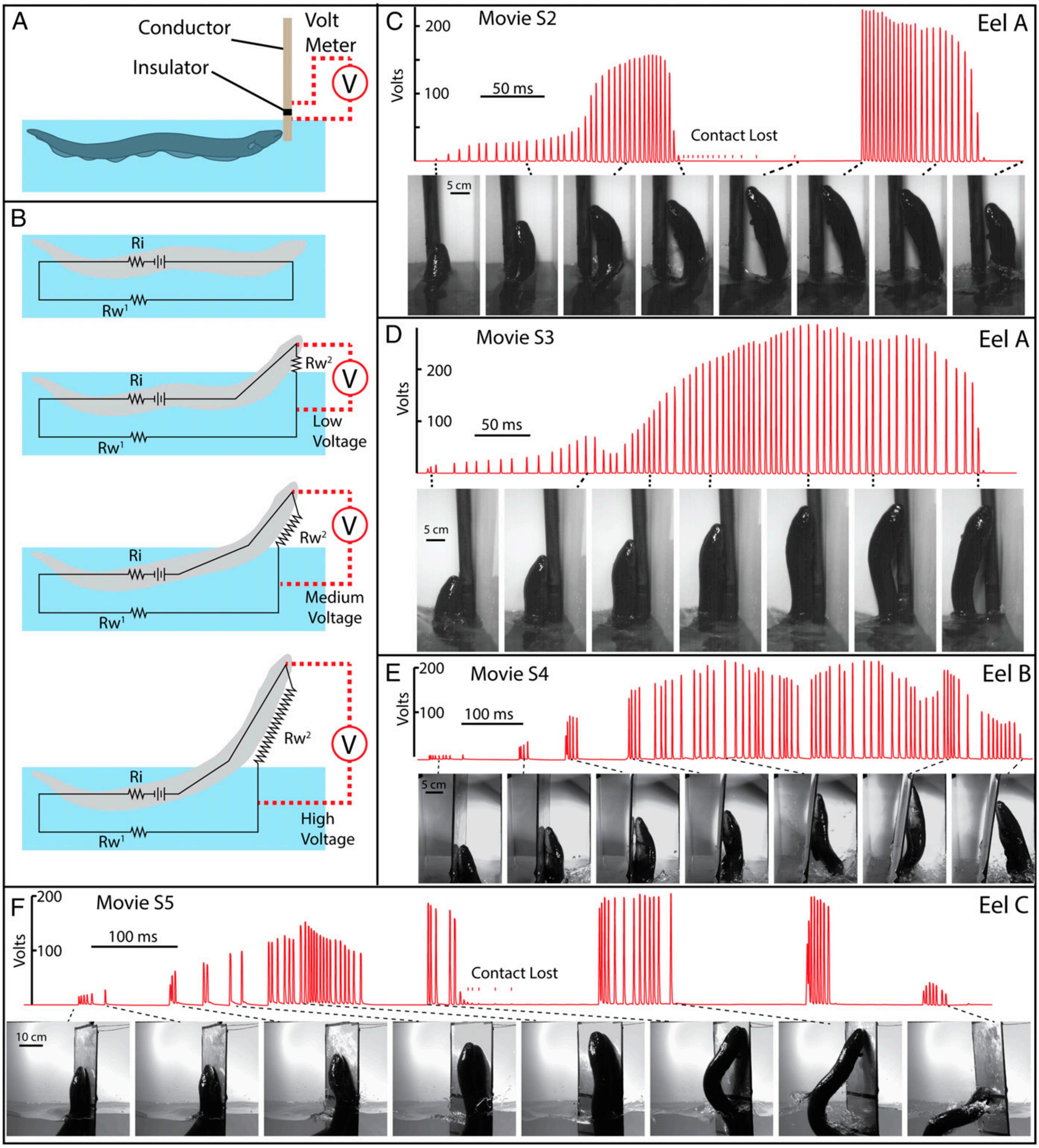

Fig. 3. Paradigm for recording voltage during eel shocking leaps. (*A*) Either a conductive carbon rod or a flat aluminum plate was split, with an insulator in between. A voltmeter (V) measured potential between the conductor in the water and the top conductor as the eel ascended. (*B*) Proposed equivalent circuit showing water resistance (*R*w1), eel internal resistance (*R*i), and a new and increasing resistance (*R*w2) for the current from head to water as the eel ascends. (*C* and *D*) Result of two trials for voltage measurement from eel A during leap, demonstrating increase in potential as the eel ascends. Note modulation of pulse rate when contact with conductor was lost (red tick-marks in *C*; see Movie S2). (*E*) Result of trial for voltage measurement from eel B during leap. (*F*) Result of trial for voltage measurement from eel C during leap. Note modulation of pulse rate when contact with conductor was lost (red tick-marks; see Movie S5).

collecting. Predators are thought to take advantage of the same opportunities (26, 32–34). Moreover, electric eels on Marajó Island reproduce during the dry season in residual water pockets, where males guard the growing larvae until the rainy season, when young eels disperse (35). Therefore, there may be a number of circumstances under which electric eels do not have an escape route or are motivated to stand their ground. Aquarium housing likely mimics the former condition.

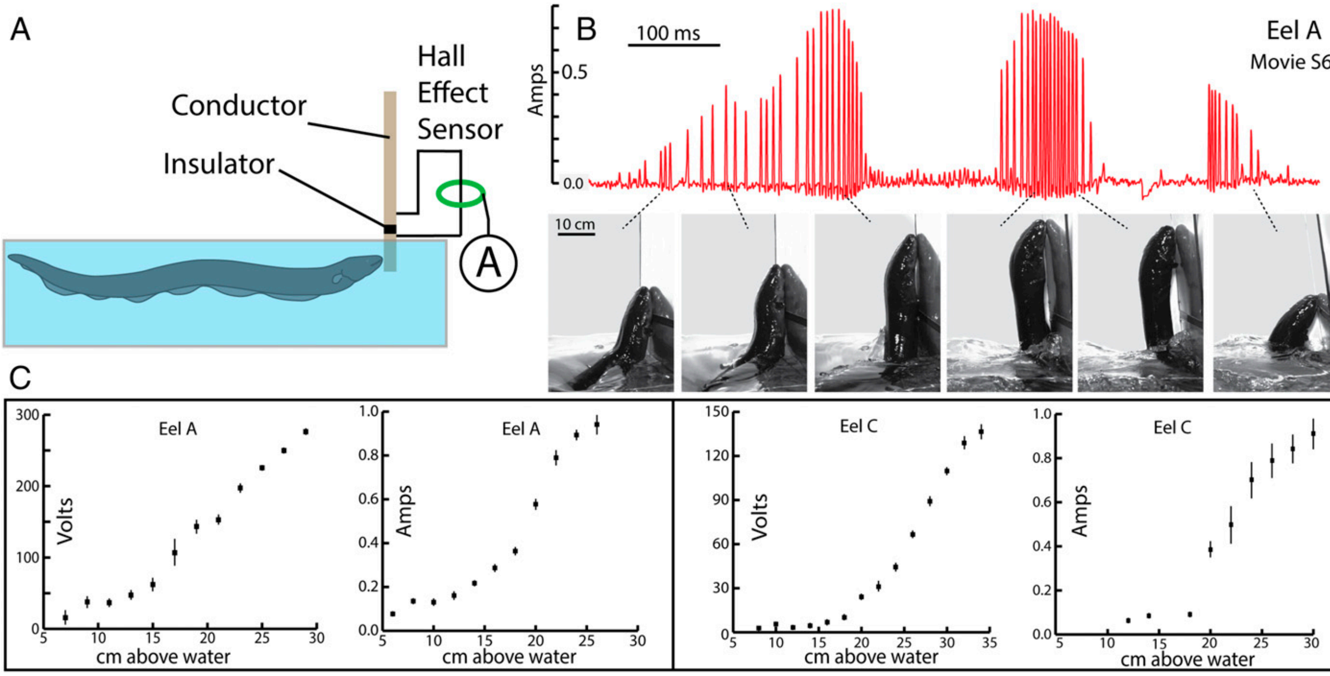

Fig. 4. Paradigm for recording current during eel shocking leap. (*A*) Two parts of a conductive aluminum plate were connected with a wire through which current was measured with a Hall effect sensor as the eel ascended. (*B*) As was the case for voltage, current increased as the eel ascended. (*C*) Comparison of current and voltage relative to eel height above water for each of two eels (five trials for each condition, eels A and C). See Movie S6 for trial illustrated in *B*.

Given that leaping from the water to shock may be risky, what advantage might this seemingly extreme behavior provide compared with discharging while submerged? Michael Faraday's "hands-on" eel experiments provide a key insight (36). In 1838, Faraday pointed out: "When one hand was in the water the shock was felt in that hand only, whatever part of the fish it was applied to; it was not very strong, and it was only in the part immersed in water" (36). Thus, despite an eel's impressive high-voltage volley, the power is distributed throughout the surrounding water and may have little effect on a terrestrial animal with only a small portion of its body submerged. A motivated terrestrial predator, harrying a trapped eel from above, may not be deterred before an eel is exhausted. Recent studies have shown that high rates of EOD are particularly costly (37). These results suggest electric eels can be vulnerable to predation. One solution is to direct the potentially limited electrical resources to the threatening target through contact. This strategy would presumably be even more important for a metabolically stressed animal with little energy to expend. The most obvious advantage of leaping is the progressive electrification of increasing portions of an animal's body, with increasing power, as the eel ascends (Movie S7). The second advantage is the potential to electrify most of a well-grounded animal (Movie S8). The latter result was reported by Sachs (18).

Although the full form of the eel's leaping behavior is astonishing, the more subtle stages by which this behavior likely evolved are apparent. Increasing power is delivered to the conductive target, first as the positive pole of the dipole field (the eel's head) is brought closer to the target, second as direct contact is made, and finally as the eel's head leaves the water and ascends the conductor. Each stage provides a progressive advantage, suggesting how it may have evolved. A similar argument has been made for the curling behavior eels use to concentrate their electric field through struggling prey (14). The effect is to cause tetanus and rapid muscle fatigue by overactivating prey efferents. In the latter case, the activation of afferent (sensory) pathways is irrelevant to the eel, but when leaping to shock large animals, the aversive sensory experience of afferent activation (combined with induced tetanus) likely plays a key role in deterrence. In this context, the eel's electrical defense may parallel the pain-inducing venoms of some insects and arachnids that have a primarily deterrent function but do not cause tissue damage (38, 39). The possibility that eels use the leaping strategy to hunt is untenable because they swallow food whole, would not benefit from stunning large animals, and never bit or tried to swallow the large conductors during or after the leap.

In light of these findings, it seems reasonable to suggest that Humboldt observed a similar eel behavior on March 19, 1800. Importantly, the events took place toward the end of the dry season, and the eels were trapped in a muddy basin, which was all that was left from a drying stream (1). Clearly, if the account is true, the eels would have deterred the horses from remaining in the pool, had the fishermen not gone to extreme measures to keep them contained. Although Humboldt's description of an eel pressing itself against the belly of one of the horses (1) does not include leaping, Schomburgk's (presumably commissioned) illustration bears a striking similarity to the eel behaviors described here (3). Robert Schomburgk knew and greatly admired Humboldt (40). Humboldt helped the Schomburgk brothers obtain funding for a trip to South America in 1840 (41), and provided at least some advice (42). However, whether the detailed illustration of Humboldt's experience (Fig. 1*A*) included any input from Humboldt or was simply the artist's interpretation may be lost to history.

It seems obvious that electric eels are the product of selection for increasing power output. This has resulted in an extraordinary animal that has fascinated scientists for centuries (9). Early investigations concentrated on understanding the nature of the electrical output and the anatomy of the electric organs (1, 2, 36). More recently, the eel's electric organs have provided key insights into biochemistry and the evolution of ion channels (43, 44). The present study is part of a recent series (12–15) that shows electric eels have been selected not only for extreme anatomical and physiological traits but also for remarkable behaviors that allow them to use electricity to maximal effect.

Methods

Eels (*Electrophorus electricus*) obtained from commercial fish suppliers were housed in custom-made Plexiglas aquariums ranging in size from 300 to 480 L with aerated water, gravel bottom, plastic imitation branches and plants, temperature between 24 and 28 °C, pH between 6.5 and 7.5, and conductivity between 300 and 400 μS/cm. Lighting was on a 12/12 light/dark cycle, and eels were fed earthworms and fish. Eel sizes were 91 cm (eel A), 66 cm (eel B), 84 cm (eel C), and 68 cm (eel D). All procedures were approved by the Vanderbilt Institutional Animal Care and Use Committee. The EODs were recorded from leaping eels by connecting a split carbon rod (3.8 cm diameter; McMaster Carr) or a split aluminum plate to wires connected to a PowerLab 8/35 data acquisition unit (ADInstruments) through a P4100 100:1 probe (Sainsmart) or a 20-dB voltage attenuator (Emerson Connectivity Solutions), with sampling at 100 k/s, and in turn connected to a MacPro laptop running LabChart 6 software (ADInstruments). As illustrated in Fig. 3, an insulator was interposed between the two conductors, and the lower conductor was moved toward the eel. When the eel ascended the conductor and passed the insulator, the voltage from head to water was measured (Fig. 3 *C–E*). At the same time, video was collected with a MotionPro HS-3 camera (Redlake) or a MotionXtra NX7S1 camera (IDT) with two RPS Studio CooLED 100 RS-5610 for lighting. Video was simultaneously recorded with a Nikon D4 SLR (Nikon) set to video mode. The high-speed camera's synchronization output was recorded on a separate PowerLab channel, allowing coordination of video and EODs. To illustrate the relationship of each high-voltage EOD to behavior in movies, each frame during which an EOD occurred was colorized in Photoshop CS 6 (Adobe Systems). The tiff format image files were then opened in QuickTime Player 7 Pro (Apple) and exported as a QuickTime movie. To record current, the same configuration was used, but the conductors were connected with wires that passed through an ACS712, 20-amp Hall effect sensor (Allegro MicroSystems, LLC). The sensor was calibrated with a TekPower TP1803D current source (Kaito Electronics). Voltages (or currents measured in voltages from the ACS712) were measured by selecting the relevant area of the LabChart 7 trace and using the "min-max" measurement function, and then using the Datapad function to collect and export the values to Microsoft Excel. To illustrate the eel's output in relationship to eel behavior, data traces were copied at high resolution from the LabChart 7 program into Adobe Illustrator and illustrated with vector graphics to allow scaling to variable final figure sizes. To allow direct observation of eel output for simulated body parts, the same electrical configuration (Fig. 3*A*) was used, except the circuit contained LEDs [wired in parallel (Fig. 1*B*) or in series/parallel (Movie S7) without resistors] that were powered by the eel's EOD. A conductive aluminum or carbon tape strip (mostly out of view for aesthetics) served as the conductor, which the eels followed upward during their shocking ascent (Movies S7 and S8).

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