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Light-Gated, Vibration-Amplitude–Dependent Action Selection in Stag Beetles: Threat Display versus Tonic Immobility

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Abstract:

Beetles, especially nocturnal Lucanidae, when confronted with danger will alternate between conspicuous threat display (head elevation, mandible opening, stridulation) and tonic immobility (TI). This review synthesizes evidence into a compact gate × branch model: light acts as an activity gate while substrate-borne vibration supplies the branching signal. Decreasing luminance opens the gate and elevates readiness; within the active state, low to moderate vibration favours display whereas high amplitudes recruit TI. The mechanistic substrate comprises highly sensitive leg mechanoreceptors—the subgenual and chordotonal organs and campaniform sensilla—whose macro- and micro-mechanical filtering encodes amplitude and spectrum. Behavioural switching shows asymmetric entry and arousal thresholds (hysteresis), explaining history-dependent onset and recovery of TI. Artificial light at night can delay, damp or mistime the gate, shifting decision boundaries for identical mechanical inputs. Additional modulators include genetic and morphological variation, energetic state, substrate transfer properties and vibrational noise. The synthesis specifies measurable axes (illuminance, peak acceleration/displacement, response class, latency and TI duration) and predicts that shielded, dim lighting with low-amplitude disturbance promotes display/locomotion whereas bright, unshielded light and impulsive shocks increase TI frequency and duration.

Keywords: Lucanidae; Response Strategy; Threat Display; Tonic Immobility; Light Gating.

1. Introduction

In nocturnal beetles—most notably the stag beetles (Lucanidae)—external cues from ambient light and substrate-borne vibration are primary drivers of state transitions between alternative defensive strategies, such as threat display (head elevation and mandible opening) and tonic immobility (TI, "death-feigning").

Field monitoring across Europe has shown that stag beetle activity is tightly anchored to twilight dynamics rather than to clock time per se, with walking and flight detections peaking around civil twilight and the early night window [1]. This pattern supports a general light-gating view of action selection: decreasing luminance acts as an external gate that elevates baseline activity and lowers the cost of moving or signalling, whereas bright conditions bias individuals towards immobility and concealment. Observations in captive contexts—where beetles become active when room lights are turned off and remain quiescent under illumination—mirror this natural light gating and help crystallise the broader question this review addresses: how do light and vibration jointly regulate the branching between conspicuous display and immobility?

Artificial light at night (ALAN) complicates this picture. Synthesising evidence across nocturnal insects, Owens and Lewis outline five principal pathways by which ALAN alters behaviour: attraction/disorientation, disruption of circadian timing, visual desensitisation and reduced contrast, altered predation risk, and interference with bioluminescent signalling (where relevant) [2]. Its ecological implications extend beyond disorientation, influencing fundamental decision-making processes in nocturnal insects. Functionally, these pathways can shift or blur decision thresholds, re-timing nightly activity and potentially changing how individuals evaluate threats. Within such altered lightscapes, the "when to be active" gate may open at atypical times or remain partially open, thereby modifying the prior with which beetles interpret subsequent mechanical cues. For a species that negotiates predation risk and intraspecific encounters via either conspicuous posturing or TI, such light-driven shifts can cascade into different allocations of time to display vs. freeze.

Whereas light sets the state gate, vibration provides the graded information that steers which action is taken once the animal is active. In a cerambycid model, Takanashi demonstrated that low-frequency (<1 kHz) substrate vibrations elicit a spectrum of rapid responses in the millisecond-to-second range—including startle jumps, stridulation (often part of threat signalling), walking, and freezing—and that the femoral chordotonal organs play a key role in mediating these outcomes [3]. Crucially, response type depends on the amplitude/spectral characteristics of the stimulus, consistent with an amplitude-dependent branching rule: lower-to-moderate intensities bias towards display or movement, whereas strong perturbations push the system towards freezing/TI. Such branching rules highlight how mechanical stimuli interact with internal state to bias behavioural outcomes.

The mechanistic substrate for this sensitivity is now comparatively well understood. The subgenual organ at the proximal tibia is among the most sensitive vibration detectors in arthropods; together with chordotonal organs within the leg and campaniform sensilla at the leg base, it forms a distributed sensor array that transduces nanometre- to micrometre-scale displacements into neural codes usable by motor circuits [4]. From a control perspective, this arrangement furnishes two essential computations for action selection: (i) robust detection of biologically salient vibrations across diverse substrates and body postures, and (ii) graded encoding of stimulus intensity that can be mapped onto different motor programs—display, locomotion, or immobility. Such graded encoding explains why small knocks to a container may evoke head-up postures, while larger impacts precipitate immobility, even in the same individual and context.

TI itself is not a binary reflex with a fixed trigger; rather, it is a context-tuned, graded phenotype. As synthesised by Humphreys and Ruxton [5], TI typically occurs late in a predation sequence and is best interpreted as a last-resort tactic whose initiation probability and duration vary with species, individual condition, and immediate context. This variability maps naturally onto threshold concepts from sensory decision theory: both the entry threshold into immobility and the arousal threshold for exiting it can be shifted by internal state and external conditions—including light level and the intensity history of recent vibration.

Bringing these strands together, we propose a concise framework for stag beetles and related Coleoptera: light provides an external gate that sets baseline activity and primes the system for certain classes of responses, while vibration amplitude supplies the branching signal that selects between threat display and tonic immobility. Under dark or low-light conditions, beetles are more likely to be in the active regime; within that regime, low-to-moderate vibrations bias towards display/locomotion, whereas high-amplitude vibrations favour immobility. Under ALAN or strong illumination, the active gate may be delayed, damped, or mis-timed, effectively shifting the boundaries between these behaviours. Framing light-gated, amplitude-dependent branching in this way yields clear payoffs: (i) it clarifies the sensorimotor basis of defensive decision-making; (ii) it situates adaptive value along a continuum of risk assessment rather than as discrete reflexes; and (iii) it offers directly translatable design cues for bio-inspired robots, where graded threat assessment can switch policies between signalling vs. passive compliance in a manner homologous to display vs. TI. The remainder of this review uses this framework to integrate structural, neuro-sensory, and behavioural evidence, while highlighting methodological standards that will make cross-study comparisons more robust [1-5].

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2. Sensory Gating and Threshold Mechanisms Underlying Defensive Strategies in Beetles

2.1 Threat display: kinematics, function, and sensory triggers

The section headings are in boldface capital and lowercase letters. Second level headings are typed as part of the succeeding paragraph (like the subsection heading of this paragraph). All manuscripts must be in English, also the table and figure texts, otherwise $_{s}w$ we cannot publish your paper. Please keep a second copy of your manuscript in your office.

Behavioural form. In stag beetles and many other Coleoptera, the threat display consists of head elevation, prothorax lifting, and mandible opening/angling, often accompanied by stridulation or body rocking. This suite of motor actions is not random but highly stereotyped. Functionally it magnifies apparent size, signals readiness to escalate, and can deter predators or rivals at relatively low cost compared with immediate flight or immobility.

Musculo-skeletal basis. The posture relies on cervical–prothoracic dorsoventral musculature to elevate the head and pronotum, mandibular adductor/abductor systems for gape control, and stiff exoskeletal leverage across the head–neck joint. The geometry of enlarged male mandibles increases visual salience yet still permits controlled elevation through favourable moment arms at the joint.

Trigger regime. At low-to-moderate substrate vibration amplitudes, animals frequently transition into display rather than freeze, sometimes adding stridulation as an acoustic/vibratory warning. This aligns with amplitude-dependent response spectra shown in cerambycids, where small mechanical inputs bias towards movement/display rather than immobility [3]. Light level gates baseline arousal: in dark/low-light states, beetles are more likely to be behaviourally available to express display [1].

2.2 Tonic immobility (TI): posture, thresholds, and adaptive logic

Behavioural form. TI (death-feigning) presents as a sudden, rigid or limp immobility with reduced spontaneous movement and often tucking of appendages. Recovery occurs after a variable latency.

Trigger regime and thresholds. TI typically follows high-intensity, near-field mechanical stimuli (firm jolts, hard knocks, grasping) or close contact with a putative predator. Comparative work shows TI is thresholded and graded: both entry and arousal thresholds shift with internal state and context [5]. This accommodates everyday observations where a light tap evokes display, but a much stronger impact elicits TI.

Neuroethological studies indicate that TI is modulated by context-dependent thresholds. Adaptive basis. TI is a last-resort tactic late in the predation sequence that can suppress pursuit or attack. Its duration and probability vary across species and individuals, consistent with a decision boundary modulated by prior stimulation and environmental conditions [5].

2.3 Photoreceptive and circadian gate: how light sets the stage

Organs and circuits. Light information enters via compound eyes (and often ocelli), is processed in optic lobes, and interacts with circadian centres that schedule activity.

Gate function. Field programmes show stag beetle activity peaks around civil twilight and early night, indicating a luminance-based gate on action readiness rather than a fixed clock [1]. Artificial light at night (ALAN) perturbs this gate via several routes—disrupted circadian timing, visual desensitisation, altered predation risk, and attraction/disorientation—thereby shifting or blurring the threshold for becoming active and, downstream, the likelihood of choosing to display vs. TI when disturbances occur [2]. These alterations not only shift behavioural timing but also reshape the cost–benefit landscape of defensive strategies.

2.4 Vibration-sensing hardware: from nanometres to neural codes

Key sensors. The subgenual organ at the proximal tibia is among the most sensitive vibration detectors in insects; leg chordotonal organs provide complementary dynamic sensing; campaniform sensilla at leg bases register load-induced cuticular strain.

Mechanical coupling and coding. These sensors mechanically couple to the substrate via the leg and deformable cuticle, enabling detection of nanometre–micrometre displacements and encoding of intensity and spectral content [4]. Functional mapping studies confirm that these sensors support both fine discrimination and rapid motor initiation. Behaviourally, cerambycids demonstrate a graded response ladder—from startle and stridulation to freezing—mediated via femoral chordotonal organs [3]. This supports a general mapping: increasing amplitude escalation from display/movement to immobility.

2.5 An integrated threshold map: light gate × vibration branch

When all components are combined, light primarily determines whether the system enters an active behavioural state or a static behavioural state, acting as a gate, while vibration amplitude serves as a branch signal, selecting specific actions in this active state. When light levels are low, the behavioural gate is more easily opened, leading to higher baseline activity and increased likelihood of movement. In this state, low to moderate vibration amplitudes typically trigger threat displays or movement, while high-amplitude vibrations are more likely to induce tonic immobility (TI). Under bright nighttime lighting or artificial light (ALAN), the gate may be delayed or weakened, reducing readiness or leading to inappropriate activation. Under these conditions, the same vibrational input may cross different decision thresholds, shifting the response toward immobility or delayed reaction time. The system may exhibit hysteresis, meaning that the threshold for entering TI may exceed the threshold for awakening from TI, introducing a history-dependent component to defensive behaviour.

2.6 What to Measure for Interpreting Prior Studies and Figures

Although this is a methods-forward review rather than an experimental paper, prior work converges on a few interpretable axes that your figures/tables can standardise across studies:

Light: report luminance/illuminance (e.g., lux) and timing relative to civil twilight [1]; Vibration: report peak acceleration or displacement and dominant frequency band; map outcomes against amplitude bins [3, 4]; Outcome metrics: binary/ordinal scoring (di·splay vs. TI), latency, and TI duration [5]; Context covariates: sex/size (weapon load), handling history, and presence of ALAN [2]. Standardising these parameters will not only facilitate cross-study synthesis but also accelerate the translation of behavioural principles into applied contexts such as bio-inspired robotics.

3. Integrated Sensory–Decision Framework for Light- and Vibration-Gated Defensive Behavior in Beetles

3.1 Information flow: from sensing to action selection

Light as a primary input signal: Standardised transect monitoring of nocturnal beetles (including stag beetles) shows that activity peaks align closely with twilight-to-night luminance changes, indicating a luminance-based gate into the active state [6]. Under artificial light at night (ALAN), nocturnal illumination can alter circadian timing and risk assessment, thereby shifting or blurring this gate [7, 8].

Vibration as a critical sensory cue: Leg mechanoreceptors—notably the subgenual organ at the proximal tibia, various scolopidial/chordotonal organs, and campaniform sensilla—form a highly sensitive array for substrate-borne vibration [9, 10], capable of encoding displacement/acceleration amplitude and frequency content [11].

Integration of sensory inputs and behavioural outputs: Synthesising available evidence indicates that light primarily determines entry into the active state (gate), while within that state vibration—via its intensity and spectrum—biases behaviour towards threat display/locomotion versus freezing/tonic immobility (TI) [6, 8, 12].

3.2 Decision boundaries: thresholds, hysteresis and history dependence

Dual-threshold structure. TI often occurs late in the predation sequence following high-intensity or near-field stimulation and exhibits a mismatch between the entry threshold and the arousal threshold (i.e., hysteresis), reflecting a decision process with history dependence [13, 14].

Amplitude–probability relation. Within the same active state, small-to-moderate vibrations commonly evoke head elevation/mandible opening or brief movement, whereas larger amplitudes more readily induce freezing/TI. Arousal from TI is likewise threshold dependent—weak vibration rarely terminates TI, whereas stronger vibration is more effective [15]. Together these features define a dual-threshold framework for entry and maintenance/exit.

3.3 State modulation: individual and contextual factors

Individual/genetic factors. In model Tenebrionidae, the propensity and duration of TI show heritable variation and trade-offs with other adaptive traits [14].

Environment. ALAN reshapes daily activity schedules and alters sensory signal-to-noise, thereby shifting the boundary between display and TI [7, 8].

Experience/history. Recent exposure to strong stimuli and the temporal structure of disturbance shift entry/arousal thresholds, such that the same amplitude can elicit different responses at different times [15].

3.4 Standardised reporting dimensions

To enhance comparability across studies, secondary syntheses and data compilations should standardise the following dimensions:

• Optical: Illuminance/luminance and time relative to twilight, to determine whether observations were made in the gate-open state [6, 7].

• Vibrational: Peak displacement/acceleration, dominant band/bandwidth, and stimulus window (impulse/sinusoid/noise); present outcomes using amplitude binning and re-

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sponse proportions [9, 10] [11].

• Behavioural: Response class (display/locomotion/freezing/TI), latency, TI duration, and arousal criteria [14, 15].

3.5 A minimally sufficient integrative model

Gate. Light environment determines entry into the active state; low light opens the gate more readily, whereas bright light/ALAN delays or suppresses it [6-8]. Branch. Within the active state, vibration amplitude governs the display vs. TI branch, with asymmetry of entry and arousal thresholds generating hysteresis [12, 15]. This model accounts for common captive observations (activity rise after lights-off; light tapping eliciting display; strong impacts eliciting TI) and provides a clear framework for evidence aggregation and identification of counterexamples in subsequent sections.

4. Conclusion

The gate × branch framework suggests that light determines readiness to act, while vibration amplitude selects the defensive programme. Contemporary lighting research indicates that artificial light at night (ALAN) modifies insect behaviour through multiple pathways; consolidating recommendations emphasise shielding, dimming, and spectrum choice to reduce disruption. Field trials further show that tailored, shielded luminaires markedly diminish nocturnal insect attraction relative to unshielded fixtures, implying that practical mitigation can restore the natural balance between threat display and tonic immobility (TI) by resetting the light gate toward darkness.

On the mechanical side, amplitude-dependent switching is consistent with the biomechanics of arthropod vibrosensation: macro-transfer through the legs and micro-filtering within subgenual/chordotonal and campaniform systems create context-specific thresholds that map graded inputs onto categorical actions. In Lucanidae, exaggerated mandibles and reinforced head–prothorax structures impose additional torque and energetic costs during escalation; such loads plausibly bias decisions toward immobility under high-amplitude shocks, while permitting conspicuous head-up displays when disturbances are mild.

Together, these lines of evidence predict that dim, shielded lighting combined with low-amplitude handling or environmental vibration should favour display/locomotion, whereas bright, unshielded illumination and impulsive shocks will increase TI frequency and duration.

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