

Mellifluous matures to malodorous in musth

Mood-altering secretions by excited male elephants smooth out social interactions.

Male Asian elephants in musth — an annual period of heightened sexual activity and intensified aggression — broadcast odoriferous, behaviourally influential messages from secretions of the temporal gland^{1–4}. From our observations in the wild, together with instantaneous chemical sampling and captive-elephant playback experiments, we have discovered that young, socially immature males in musth signal their naivety by releasing honey-like odours to avoid conflict with adult males, whereas older musth males broadcast malodorous combinations to deter young males, facilitating the smooth functioning of male society. As elephant–human conflicts can upset this equilibrium, chemically modulating male behaviour may be one way to help the conservation of wild elephants.

During musth in adult male Asian elephants (*Elephas maximus*; Fig. 1), serum pH is raised and androgen synthesis, ketogenesis and lipid catabolism all increase^{2–4}. These physiological alterations are reflected in malodorous secretions that stream from the elephant's unique temporal gland⁴.

Ancient Hindu poetry describes the arrival of bees to “gather sweetness from the temples of [young] musth elephants”⁵.

In keeping with this poetic observation, we were struck by the powerful honey-like odour emitted by a captive 11-year-old male Asian elephant when he began secreting. This youthful musth was termed ‘moda’, a period that is characterized by mischievous and erratic behaviour⁶. We therefore investigated whether the extensive dual olfactory systems of male Asian elephants can differentiate between youthful musth chemical signals and those from sexually and socially mature males.

We analysed the changing chemical composition of temporal-gland secretions from young post-pubertal male Asian elephants, who were exhibiting episodes of aberrant behaviour and had fluctuating hormone levels (Table 1). Combining innovative modification of solid-phase micro-extraction⁷, capture of headspace volatiles in evacuated bottles⁸, and chemical analysis by gas chromatography with mass spectrometry^{7,8}, we identified the predominant components in the mellifluous exudates as 3-hexen-1-ol, two ketones (2-heptanone and acetophenone) and various acetates (mainly isoamyl acetate) — all of which are sweet-smelling (Table 1). There is a marked chemical convergence between the temporal-gland secretions of male Asian elephants in



Figure 1 A mature musth male takes a swim to cool off. During musth, secretions emanate from the temporal gland near the eye.

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moda musth, and honeybees and honey — honey also contains 3-hexen-1-ol and sweet-smelling acetates, and bees use pheromone blends containing 2-heptanone and acetates, including isoamyl acetate⁹.

As males mature (post-moda), their periods of increased androgen hormone levels lengthen, aggressive behaviour becomes overt, and their copious secretions are chemically altered to resemble those of the adult temporal gland³ (Table 1). Concentrations of 3-hexen-1-ol and acetates are greatly reduced, and acetophenone is replaced by a foul-smelling combination of 2-nonanone, acyclic ketones and substituted cyclohexanones, including 3-methyl-2-cyclohexen-1-one and frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane)^{4,8}. These last two compounds are also secreted together as pheromones by bark beetles (*Dendroctonus tenebrans*)^{10,11}.

‘Playback’ experiments monitoring the responses of captive males to collected samples of temporal-gland secretions, together with observations of the behaviour of wild males of known chemical status, supported our idea that chemical signals change in association with maturing musth-linked behaviours. Moda males generally avoided the secretions of older males, whereas samples from moda males elicited little response from mature individuals (Table 1, and see supplementary information).

Encounters observed in the wild between a focal musth male, emitting chemically characterized adult secretions, and 12 different male conspecifics, emitting varying chemical signals, were consistent with our results from elephants in captivity. After sniffing the focal musth male from distances of 3–100 metres, three juveniles showed little reaction, five young males acquiesced, and four were apprehensive, choosing to avoid the senior male.

When the smell of a chemically defined moda male was assessed from a distance by

Table 1 Temporal-gland secretion signalling by elephants in musth

Male elephants	Honey moda	Post-moda	Older adult musth
Age (years)	8–13	14–18	25–35
Behavioural status†‡	1.0 (1.0–4.0)* ^{1,2}	17.5 (10.0–25.0)* ²	34 (32.0–39.0)* ¹
Serum androgens (ng ml ⁻¹)†§	13.2 (10.3–16.8)* ¹	21.9 (11.0–30.0)* ²	36.7 (31.9–65.6)* ^{1,2}
n, NS	4, 32	4, 14	6, 18
<i>TGS compounds</i>		<i>Concentration (g m⁻³)</i>	
Esters†	10.5 (8.5–13.5)¶	ND	ND
3-Hexen-1-ol†	30.0 (8.5–13.5)	ND	ND
Acetophenone†#	2.0 (1.05–2.15)* ^{1,2}	0.15 (0.1–0.2)* ²	0.095 (0.06–0.10)* ¹
Frontalin†‡	ND	0.10 (0.10–0.12)*	0.22 (0.20–0.30)*
2-Nonanone†\$	ND	0.10 (0.05–0.10)*	0.23 (0.21–0.30)*
<i>State of responder</i>		<i>TGS playbacks</i>	
Moda (n = 3)	89% attracted (3 tests)	NT	80% repelled (5 tests)
Adult (n = 3)	78% no response (3 tests)	NT	33% attracted 33% no response 33% repelled (5 tests)

Behavioural and chemical evidence for signalling using temporal-gland secretion (TGS) by male Asian elephants (median, 25–75%) during moda and adult musth states (see supplementary information). n, number of elephants; ND, not detected; NS, number of samples; NT, not tested. Asterisks represent significant results.

†Median (25–75%).
‡Scored 0 (no deviation from normal) to 5 (maximum deviation from normal); P < 0.05. *DR (difference of ranks) = 37.9, Q = 6.99; **DR = 23.9, Q = 4.05.

§P < 0.0001, d.f. = 2, H = 28.8. *DR = 29.33, Q = 5.35;

**DR = 21.60, Q = 3.26.

¶Number of esters (see supplementary information).

||Detectable limit is > 1 part per billion volume.

#P < 0.0001, d.f. = 2, H = 48.9; *DR = 35.37, Q = 6.46;

**DR = 27.65, Q = 4.66.

‡XU = 74, P < 0.003 (see supplementary information).

\$U = 74, P < 0.0001.

Kruskal–Wallis ANOVA, Dunn's pairwise multiple comparison (§#);

Mann–Whitney U-test (‡\$).

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the focal male, it was ignored, suggesting that the honey odour conveys a non-threatening message. However, the focal male stalked and attacked a different, slightly secreting young adult in a dominance interaction (see supplementary information). It is evidently advantageous to be able to recognize the ontogenic degree of musth in conspecifics before initiating physical encounters^{3,12,13}.

Unravelling this medley of chemical signals helps to clarify the behavioural and physiological mechanisms that underlie the phenomenon of musth and its influence on other males. This knowledge should help in the formulation of deterrence programmes in southern India against crop-raiding wild elephants, most of which are male and are often in musth. Moreover, the moda-musth emanations of young maturing elephants, as poetically observed by the ancient Hindus, have now been substantiated by modern scientific techniques.

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