Review

Musth and sexual selection in elephants: a review of signalling properties and potential fitness consequences

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Received 23 February 2021; initial decision 30 May 2021; revised 22 July 2021; accepted 9 August 2021; published online 17 September 2021

Abstract

Sexual selection mediated by multimodal signals is common among polygynous species, including seasonally breeding mammals. Indirect benefit models provide plausible explanations for how and why mate selection can occur in the absence of direct benefits. Musth — an asynchronous reproductive state in male elephants — facilitates both inter- and intrasexual selection via indirect benefits, and it is further communicated through a multimodal signal. In this review, we synthesise existing evidence that supports the hypothesis that musth is a multimodal signal subject to sexual selection and that male elephants increase their direct fitness by propagating this signal while females accrue indirect benefits. Musth is characterised by a suite of physiological and behavioural changes, serving to facilitate copulation between the sexes, and via multisensory modalities musth conveys honest information about the condition of a male. Female elephants mate preferentially with musth males, increasing their own fitness in the absence of direct benefits. In addition, musth resolves dynamic dominance hierarchies among male elephants and often eliminates the need for costly physical combat. Future work in this field should investigate potential postcopulatory selection mechanisms in elephants, including sperm competition and cryptic female choice. These
topics join other fundamental questions related to sexual selection, signalling, and indirect benefits that are still unanswered in elephants.

**Keywords**

Elephas maximus, indirect benefits, intersexual selection, intrasexual competition, Loxodonta africana, Loxodonta cyclotis, mate choice, multimodal signal.

**1. Introduction**

Since Charles Darwin’s exploration of the theory in ‘The Descent of Man, and Selection in Relation to Sex’ (1871), biologists have shown keen interest in sexual selection (Maynard Smith, 1991; Andersson, 1994; Jones & Ratterman, 2009). The driving forces behind sexual selection — principally intra- and intersexual selection — can occur simultaneously (Hosken & House, 2011). Examples of sexual selection abound in polygamous species including many mammals, where operational sex ratios are unbalanced (Clutton-Brock, 2016). These species exhibit sexual dimorphism, including in size; larger males are typically selected for their competitive abilities and capacity to enter or maintain an enhanced reproductive state (Ralls, 1976; Isaac, 2005). Sexual size dimorphism is common in cases where the choosier sex accrues immediate, direct benefits from their chosen mates, such as access to physical resources or protection (Jones & Ratterman, 2009). However, indirect benefit models of sexual selection posit that sexually selected traits in one sex (usually males) evolve due to choices that provide no immediate but rather delayed benefit to the opposite sex (usually to females in the form of genetic quality for the offspring, or genes that make the offspring attractive mates), and these models are well-supported in the literature (Maynard Smith, 1991; Dawkins & Guilford, 1996; Kokko et al., 2003; Andersson & Simmons, 2006; Kotiaho & Puurtinen, 2007; Hosken & House, 2011).

Animals can use signals and/or indices to convey information about mate quality, especially when indirect benefits may be accrued by the choosier sex (Maynard Smith & Harper, 1995, 2003). Potential mates and competitors may assess qualities of conspecifics via multimodal signals, those that are propagated and/or received via multiple sensory channels (Higham & Hebets, 2013; Schaefer & Ruxton, 2015). Multimodal signals are taxonomically widespread and help ensure a sender’s message is accurately conveyed to a receiver (Partan & Marler, 1999; Higham & Hebets, 2013), and/or these overlapping signal components provide nuanced information or elicit a new
response when they are combined (Møller & Pomiankowski, 1993; Johnstone, 1996). Selection for multimodal signals has been described in a wide range of taxa, including mammals (Taylor et al., 2007, 2011; Uetz et al., 2009; Barry et al., 2010; Taff et al., 2012; Uy & Safran, 2013). A well-known example of a sexually selected trait with multiple signal components is rut, a heightened reproductive period in some seasonally breeding ungulates (Mysterud et al., 2004; Pelletier & Festa-Bianchet, 2006). In these species, food resources and mating potential are seasonal; both sexes focus reproductive efforts simultaneously, making competition for mates intense. At least partly to advertise reproductive state, rutting species have evolved multimodal signals, including antlers and horns (visual signals), vocalizations (acoustic signals), and/or distinct odours (olfactory signals), all of which are directly linked to the health, status, and/or condition of the sender (Clutton-Brock & Albon, 1979; Berglund et al., 1996; Miller et al., 1998; Martín et al., 2014).

‘Musth’ is a male reproductive condition that is unique to elephants and functions via multimodal signals that facilitate sexual selection (Eisenberg et al., 1971; Jainudeen et al., 1972b; Poole & Moss, 1981; Poole, 1987; Poole, 1989a). While similar to rut, musth is distinct from other sexually selected traits in mammals; it is asynchronous but also regularly occurring, is likely influenced by a range of intrinsic, environmental, and social pressures, and acts to signal reproductive intent to conspecifics of both sexes, providing information about mate quality (intersexual selection) and competitive ability (intrasexual selection) (Figure 1). Long-lived, socially complex species may be expected to show extreme flexibility in their reproductive strategies, and on its surface, the role of musth is deceptively simple: males signal intent through musth to resolve dominance hierarchies and communicate a heightened reproductive state. However, musth is a more complicated reproductive strategy, with facets encompassing intersexual selection, intrasexual competition, and indirect benefits.

Musth is observed in all three extant elephant species: Asian elephants (*Elephas maximus*), African savanna elephants (*Loxodonta africana*), and African forest elephants (*L. cyclotis*). All three species are polygynous with males dispersing from their natal herds around the time of sexual maturity to form looser aggregations (Table 1). Males first undergo musth in early adulthood (about 20–30 years) to effectively advertise their reproductive state and potential fitness to conspecifics (Jainudeen et al., 1972a; Poole et al., 1984; Poole, 1987), and musth is characterised by an alteration
Figure 1. Concepts related to sexual selection and musth in elephants. Solid lines indicate direct links between concepts, and dashed show indirect links. Arrows show directionality of these connections. Blue boxes represent factors that may affect key properties of musth, including intensity, frequency, and duration. Orange boxes show the sensory channels that may be communicated separately or in combination to signal musth. The green box describes properties of the male elephant that may be communicated via musth (also affected indirectly by intrinsic factors of the male). Pink boxes indicate the interrelated implications of musth in terms of inter- and intrasexual selection. Concepts with sparse, conflicting, and/or absent empirical support currently, but which we suggest should be further investigated, are italicised and marked with an asterisk (\*).
Table 1.
Generalised age classes for male elephants.

| Age class     | Age range (years) | Description                                                                 |
|---------------|-------------------|-----------------------------------------------------------------------------|
| Calf          | 0–1               | Closely associated with mother.                                             |
| Adolescent    | 2–5               | Commonly extends associations to other members of nuclear family.           |
| Prepubescent  | 6–10              | Frequently observed at the periphery of nuclear family.                     |
| Postpubescent | 11–15             | Generally separate from nuclear family, but maintains some contact.         |
| Young adult   | 16–20             | Disperses from nuclear family, forming smaller, more temporary ‘bachelor’ group(s) with other young adults. |
| Adult         | 20–30             | Mostly solitary, but may retain membership in bachelor group(s).            |
| Mature adult  | >30               | Sexual peak in 30s. Do not associate with other mature adults; can be completely solitary or associate with younger bachelor groups. |

Age ranges and descriptions adapted and modified from McKay (1973), Moss & Poole (1983), Sukumar (1989), Poole (1994), Arivazhagan & Sukumar (2008), Evans & Harris (2008), and Lee et al. (2011). Note that there are likely inter- and intraspecific variation in age class designations and ranges.

in a male’s hormonal profile (e.g., elevated testosterone) with concomitant behavioural changes including those with signalling implications. Musth is frequently cited as a classic example of sexual selection and honest signalling linked to the physiological condition of the sender (Maynard Smith & Price, 1973; Andersson, 1994; Maynard Smith & Harper, 2003). Darwin himself described the influence of musth on elephant social organization and sexual signalling in ‘Descent of Man’ (1871) with further emphasis in general texts on sexual selection since then (e.g., Andersson (1994), Clutton-Brock (2016)). Further, the musth signal occurs over multiple sensory modalities (i.e., visual, acoustic, and chemical channels), and even though we can make assumptions about how each channel may effectively communicate musth, it is unclear if these sensory components operate together (e.g., the message changes with various combinations of these channels) or to what extent these components still have functionality when they are isolated.

Accepting that musth evolved under intra- and inter-sexual selection, fundamental questions related to sexual selection remain to be answered in elephants, including the roles of the sensory components of the musth signal
(visual, auditory, and chemical channels) and the existence or value of indirect fitness benefits. The purpose of this review is to summarise the current evidence that musth is a multimodal signal shaped by sexual selection and to pose further possibilities for research not often explored in large, long-lived mammals; we provide possible explanations for how elephants utilise multiple sensory channels in the musth signal and why depending on musth as a sexual signal could have evolved via inter- and/or intrasexual selection. We begin with a brief summary of the social organization of elephants, emphasizing how social and behavioural pressures set the stage for the evolution of the musth signal. Next, we describe what the multiple sensory elements of the musth signal are, why each modality may be utilised, and how these components may interact and contribute to the honesty of musth as a signal. We then synthesise the existing evidence from recent studies of elephants with emerging indirect benefits models of sexual selection to outline why musth may have evolved with distinct fitness benefits for males and females. We conclude with potential lines of inquiry that can address the remaining questions surrounding musth, including postcopulatory selection.

2. Elephant social organization

Elephants are well-known for their long-lasting relationships among kin, complex social interactions, and other gregarious behaviour that is similar to many primates and other social species (Sukumar, 2003; de Silva & Wittemyer, 2012). These qualities are best described for African savanna elephants (henceforth simply referred to as ‘African elephants’ unless otherwise designated, despite evidence that L. africana is distinct from L. cyclotis), but they generally unite the three extant elephant species. Elephant social structures centre around females. Female elephant social organization is maintained by fission-fusion processes with groups merging or splitting with changes in resource availability. However, unlike most other fission-fusion species, elephant dominance hierarchies are multileveled, especially in African elephants (Wittemyer et al., 2005; Archie et al., 2006; Wittemyer & Getz, 2007; de Silva & Wittemyer, 2012). Female African elephants are philopatric and retain close bonds with their natal groups for life (Moss & Poole, 1983; Wittemyer & Getz, 2007; Fishlock & Lee, 2013; Schuttler et al., 2014) while Asian elephants have smaller and less coherent groups (Fernando & Lande, 2000; de Silva et al., 2011, 2017; Nandini et al., 2018).
Once thought to be solitary upon leaving their natal groups, evidence illustrates that male elephants exhibit both short- and long-term connections with each other, some of which are based on kinship and may rival female relationships in terms of complexity (Chiyo et al., 2011a, 2014; Srinivasiah et al., 2019; Keerthipriya et al., 2020; Keerthipriya et al., 2021). After leaving their natal groups, young adult male African elephants form loose relationships with each other, often in the company of a mature male, perhaps facilitating the exchange of social and ecological knowledge (Table 1) (Evans & Harris, 2008; Goldenberg et al., 2014; Allen et al., 2020). Similar male relationships also occur in Asian elephants, although younger males rarely associate with older males, and just as in females, these networks are smaller and more variable over time (Keerthipriya et al., 2021).

Both intersexual selection and intrasexual competition are characteristic of many polygynous mammal societies (Clutton-Brock, 2016). Any stable male–female associations in adult elephants are relatively rare outside periods of reproduction primarily because the sexes are spatially segregated during adulthood (Table 1). This social organization is reflected in the sexual dimorphism present in all three elephant species, including in body size and the presence and/or size of tusks (Shoshani & Eisenberg, 1982; Sukumar, 2003; Shannon et al., 2006a). Although males reach sexual maturity around 10–12 years of age, they do not generally reach their sexual peak until their thirties (Laws, 1969; Poole, 1987; Sukumar, 1989; Poole, 1994; Turkalo et al., 2017). Females become sexually mature between 8 and 12 years, and are in oestrus for only four to six days every four to five years — assuming they conceive each time they are sexually receptive and ovulate (Sukumar, 1989, 2003; Freeman et al., 2009; Moss et al., 2011; Brown, 2014). As such, males often engage in contest competition for access to receptive females, potentially year-round depending on female receptivity (Poole, 1989a; Sukumar, 1989; Vidya & Sukumar, 2005; Keerthipriya et al., 2020). Female elephants should exert a high degree of intersexual selection to choose an appropriate mate because fecundity in elephants is low (Seth-Smith & Parker, 1967; Thapa, 2009; Moss et al., 2019); there is much investment in offspring with exceedingly long interbirth intervals (gestation is 20–22 months, and weaning occurs at 3–5 years) (Moss, 1983; Lee & Moss, 1986; Chelliah & Sukumar, 2015). Both inter- and intrasexual selection set the stage for a signal that maximises fitness gains while minimizing costs in animals searching and competing for mates (Maynard Smith & Price, 1973; Clutton-Brock, 2016). In male elephants, this sexually selected signal is musth.
3. Musth: multimodal signalling mechanisms

To announce their reproductive intent, sexually mature male elephants undergo musth, a heightened reproductive period that occurs regularly — and most often asynchronously — within populations (Eisenberg et al., 1971; Poole, 1987; Ananth, 2000). The timing of musth varies within and between males, which is the primary distinguishing factor from similar phenomena in seasonally breeding mammals like the synchronous rutting season observed in many ungulates (Eisenberg et al., 1971; Lincoln & Guiness, 1973; Poole, 1987; Clutton-Brock, 1989). Only males with high enough body conditions can enter musth (Jainudeen et al., 1972b; Chandrasekharan et al., 1992). The state begins with a surge in serum androgens (e.g., testosterone, dihydrotestosterone) and is partially regulated by adrenal and thyroid functions (Jainudeen et al., 1972a; Hall-Martin & van der Walt, 1984; Poole et al., 1984; Rasmussen et al., 1984, 1996; Cooper et al., 1990; Niemuller & Liptrap, 1991; Brown et al., 2007; Brown, 2014; Chave et al., 2019) — the concentrations of these hormones contribute to the duration of a musth episode and therefore the amount of access to receptive females (Ganswindt et al., 2005a, 2010; Yon et al., 2007). Social and age-dependent factors influence androgen concentrations: older, more dominant males exhibit higher testosterone levels (Lincoln & Ratnasooriya, 1996; Ganswindt et al., 2010), connecting a male’s health status, social dominance, and reproductive potential (Rasmussen et al., 2008a; Keerthipriya & Vidya, 2019). These hormonal changes trigger a suite of physiological transformations, which are thought to reflect a male’s metabolic state and also influence the chemical signals males can release during musth (Silva & Kuruwita, 1993; Dickerman et al., 1994; Rasmussen & Perrin, 1999; Schulte & Rasmussen, 1999). For intra- or inter-sexual selection to occur, there must be variation in a sexually selected trait among potential competitors or mates for conspecifics to assess (Andersson, 1986, 1994; Andersson & Simmons, 2006). In elephants, the internal physiological changes causing musth in turn affect external musth indicators and multimodal signals (e.g., behavioural changes, secretions and excretions), thereby honestly advertising a male’s reproductive state, facilitating assessment by conspecifics (Rasmussen et al., 1984, 1996; Rasmussen & Schulte, 1999).

Androgens also initiate pronounced behavioural changes during musth, many of which have signalling functions. Musth males exhibit distinct temporal gland secretions (on either side of the head) and streams of urine that
Figure 2. Adult male Asian elephant (*Elephas maximus*) in musth, surrounded by adult and subadult female elephants, in Minneriya National Park, Sri Lanka. Note visible temporal gland secretion on side of head and dark stains from urine dribbling on rear legs. Photo by C. LaDue.

leave stains on the body (Figure 2). These secretions contain chemicals with signaling potential especially in mid- to late stages of musth (Jainudeen et al., 1972a; Poole & Moss, 1981; Rajaram & Krishnamurthy, 2003). In addition to acting as visual indications of musth, these exudates increase the duration that they can serve as meaningful chemical signals. Poole (1987) described musth behaviour in wild African elephants in Amboseli National Park, Kenya, including increased aggression, ear waves, trunk curls, an exaggerated ‘musth walk’, and pronounced body posture. Similar behaviours have been noted in Asian elephants (Schulte & Rasmussen, 1999; Rajaram, 2006; Keerthipriya et al., 2020) and in other African elephant populations (Hall-Martin, 1987; Kahl & Armstrong, 2002; Ganswindt et al., 2005b; Rasmussen et al., 2008a). African elephants also produce a distinct, low-frequency ‘musth rumble’, evidence of a long-distance component to the musth signal (Poole et al., 1988; Poole, 1999). Whether there are acoustic calls unique to musth in Asian elephants is still being investigated (de Silva, 2010; Stoeger & de Silva, 2014). These components operate across a range of temporal and spatial scales, perhaps ensuring that a male in musth announces
reproductive intent over complex environmental gradients (Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011).

Visual signals provide information between senders and receivers over short ranges and timescales. There are certainly visual components of the musth signal — including the conspicuous musth walk, head shakes, trunk curls, false charges, and thrashing of vegetation (Poole, 1989a; Kahl & Armstrong, 2002) — but these may be by-products of other behavioural changes or displacement behaviours, as elephant vision is somewhat poor especially at range (Stone & Halasz, 1989; Murphy et al., 1992). For example, ear flaps that are characteristic of alertness or threat displays in other contexts may increase in frequency during musth simply to help transmit chemical signals from the temporal glands through the air (Poole, 1989a; Kahl & Armstrong, 2002). The more conspicuous visual components (e.g., musth walk, charging) may be stronger signals, and in many cases these seem to be linked to ritualistic displays preceding physical combat. Therefore, the functionality of musth to mediate intrasexual competition may be facilitated at least in part by visual signals. Still, the physical habitat also plays a role; visual signals may be of little utility over long distances, at night, or in forested landscapes that some elephant populations of each species inhabit. As such, musth behaviours with visual signalling components may have varying levels of relevance at local or regional scales.

Acoustic signals, especially those of low frequency, may be more efficacious; they can be propagated over long distances and operate in a variety of social and reproductive contexts (Leong et al., 2003; Garstang, 2004; Leighty et al., 2008; Stoeger & Baotic, 2016). Playback experiments have shown that male and female African elephants respond to male rumbles according to the musth status of the sender (and males respond differently based on their own musth and social status) (Poole, 1999). Vocal signals may be inherently honest because they vary directly with qualities of the sender such as overall body size (Fitch, 1997; Riede & Fitch, 1999; Reby & McComb, 2003), and so in elephants conspecifics may be using musth rumbles to assess the size and/or quality of the sender (Herbst et al., 2012). Communicating these conditions would be relevant both for reducing intrasexual competition and initiating intersexual interactions, especially when visual contact is impossible. Furthermore, these vocal signals may also have flexibility across both open areas (where sightlines are present, but elephant density may be low) and forested landscapes (where sightlines are absent, but elephant density
is higher). However, forests can severely attenuate higher frequency sounds, and so acoustic signals may be less effective in *E. maximus* and *L. cyclo-tis* (Garstang, 2004; Stoeger & de Silva, 2014; Hedwig et al., 2018). Furthermore, it is unclear if *L. africana* musth males are uniquely capable of producing musth rumbles or if there are sufficient costs that dissuade males from using the musth rumble outside of musth; if visual or chemical validation of these vocal musth signals are impossible, then perhaps they may not exist at all. Indeed, acoustic components unique to the musth signal in Asian elephants are yet to be systematically identified. Continued comparative investigations into elephant vocal communication will elucidate the selective forces that shape acoustic signalling during musth and other social interactions (Pardo et al., 2019; Stoeger, 2021).

Perhaps more than any other sensory modality, elephants rely on olfaction, and it seems to be the most important and independent of the musth signal components (Rasmussen, 2003). Chemical signals have distinct advantages over signals of other sensory modalities, as they can be produced in small quantities yet have long-lasting effects even if the original sender is absent. For example, oestrous females may use chemical signals left behind by musth males to locate a suitable mate during their limited time of receptivity. Furthermore, quantifying the variation in chemical signal production in vertebrate populations is increasingly feasible for researchers to better understand whether and how the choosier sex uses these chemicals to assess mate quality (Müller-Schwarze, 2006; Johansson & Jones, 2007; Apps et al., 2015). Male elephants produce exudates with signaling potential continuously throughout musth, including via temporal gland secretions, urine dribbling, breath, and possibly even faeces (Rasmussen, 1988; Rasmussen & Krishnamurthy, 2001; Rasmussen & Greenwood, 2003; Hollister-Smith et al., 2008; Ghosal et al., 2012).

For Asian elephants, frontalin has been identified as the musth pheromone (Rasmussen & Greenwood, 2003). Sexually mature males produce frontalin during musth, increasing the concentration of the pheromone produced and released with successive musth episodes (Rasmussen et al., 2002) and, in conjunction with other compounds, even within a single musth period (Rasmussen et al., 1990). Responses to frontalin are dependent upon intrinsic properties of the receivers (LaDue et al., 2018), as predicted by sexual selection. For example, subadult males are repelled by frontalin, whereas receptive females are attracted to frontalin much more than non-receptive
females (e.g., those that are pregnant) (Rasmussen & Greenwood, 2003). Similarly, in the absence of the signaller, the responses to male temporal gland secretions depend on the musth status of the receiver; commonly, musth males react to the exudates of other musth males with apprehension and/or exploratory and contact behaviour (Rasmussen et al., 2002). Pheromone production and response patterns follow predictions set forth by sexual selection theory; males produce frontalin in a manner that is consistent with their condition (e.g., musth status) (Greenwood et al., 2005; Riddle et al., 2006), and conspecifics respond appropriately based on properties of the signal and their own condition (LaDue et al., 2018). Further, the chemical composition and concentration of musth exudates (including frontalin) in Asian elephants changes both with the age of the sender and as a single musth episode progresses through early, middle, late, and ending stages (Greenwood et al., 2005; Riddle et al., 2006). Additionally, before a male is sexually mature (termed ‘moda musth’) the chemical composition of temporal gland secretions in Asian elephants is distinct from secretions in early and late adulthood (Rasmussen et al., 2002), which may be correlated with age-related serum androgen levels. These shifting chemical signals may reflect changing selective pressures operating at different stages of musth, indicating that a male’s musth status is not binary (i.e., restricted to either musth or non-musth phases) (Jainudeen et al., 1972a; Poole, 1987; Scott, 2002; Ganswindt et al., 2010). However, the relevance of shifting chemical signals and selective gradients have yet to be studied in wild populations of Asian elephants, African elephants, or via other sensory modalities. Still, the fact that frontalin and other chemical compounds elicit a suite of behavioural responses from both sexes illustrates its role in female mate choice and intrasexual competition in Asian elephants.

A musth pheromone operationally similar to frontalin has yet to be chemically identified in *Loxodonta* spp., but there is behavioural evidence that one exists. For instance, the chemical composition of the temporal gland secretions of Asian and African elephants in musth are similar (Rasmussen et al., 1996). Additionally, wild female African elephants react more strongly, sometimes vocalizing, to urine left by musth males compared to the urine of non-musth males or females (Poole, 1987). Response of captive male African elephants differ between musth and non-musth urine, and are influenced by age, dominance status, and social access (Hollister-Smith et al., 2008) in ways that are predicted via intrasexual competition. Further, the chemical
composition of urine, which includes compounds known to have signalling value in other species, changes as a male elephant ages, as he enters musth, and even after the signal is deposited (Rasmussen & Wittemyer, 2002; Goodwin et al., 2012). The interspecies similarities in the production of distinct chemical signals during musth (i.e., temporal gland secretions and urine dribbling) emphasise the value of these signals to conveying the musth message to conspecifics, and they seem to be most effective in communicating between conspecifics of different sexes, ages, and reproductive statuses over broad spatial and temporal scales.

Perhaps we may assume that the multimodal nature of musth increases redundancy to ensure accurate reception from the receiver(s), even though the interactions effects of these sensory modalities that occur during musth have not yet been systematically studied. Signal theory offers predictions for how these sensory interactions may change depending on habitat (Searcy & Nowicki, 2005), offering signalling flexibility across a range of environments. For example, in open landscapes where elephant density is low, chemical and auditory signals from a musth male may work together over long distances to attract oestrous females and deter potential male competitors. When elephants encounter each other in these habitats, visual signals may be used to validate message(s) received from the olfactory and/or auditory components. This prediction is supported by the fact that sexual size dimorphism is more pronounced in the savanna-dwelling *L. africana* compared to the forest-dwelling *L. cyclotis*, and full-grown male *L. africana* tend to be larger than in *L. cyclotis* (Lee & Moss, 1995; Morgan & Lee, 2003). Therefore, a younger *L. africana* male in particular that inhabits open landscapes may benefit by validating the size of an older male, especially if the older male is at the end of his musth (and therefore may have lost weight) and the younger male is just beginning his musth cycle. Conversely, in forested habitats, the chemical and auditory signals may validate each other to facilitate mate selection and conflict avoidance, making visual information less important. In forested areas where elephants are more densely distributed, visual validation may also be less important if mates are readily available. If musth males emit a specific rumble to communicate their status, females can locate these males with the auditory signal, and because rumbles are associated with body size, non-musth males can also use these signals to assess a potential threat (Stoeger & Baotic, 2016; Baotic & Stoeger, 2017). Both males and females would then be able to use chemical signals to validate the
auditory signals. Indeed, the chemical signals may be more valuable because they persist longer. If these predictions hold true, both habitat and receiver sex/status could influence the strength of the interactions between the sensory modalities that comprise the musth signal, thereby explaining how and why multiple components of the musth signal exist.

Musth is accompanied by distinct physical and behavioural changes in male elephants that serve to announce reproductive intent to conspecifics of both sexes. Physiological changes within musth males facilitate the production of an inherently honest, multimodal signal, covering visual, auditory, and olfactory sensory modalities. The information provided by the signal(s) sets the stage for musth to serve important roles in both mate choice and intrasexual competition.

4. Intersexual selection, male–male competition, and indirect benefits

As a signal, musth in elephants is itself a trait subject to sexual selection. However, similar to any other sexually selected trait, the occurrence of musth should be linked to variation in reproductive success (Hosken & House, 2011). Elephants are polygynous and do not defend distinct territories, nor do adult male elephants typically associate with females beyond the period of oestrus (Poole, 1989b; Ganswindt et al., 2005b; Vidya & Sukumar, 2005; de Silva & Wittemyer, 2012). Therefore, it is unlikely that females choose to mate with musth males as a result of a direct benefit, such as parental care, protection, or access to resources within a territory (Møller & Jennions, 2001; Jones & Ratterman, 2009). However, existing evidence and prevailing hypotheses on sexual selection suggest that indirect benefits may have led to the evolution of musth as it is observed today. If we assume these indirect benefits exist in the case of elephants, reproductive success of offspring from a female that mates with a musth male is greater. Males must be able to maintain high body condition themselves to remain in musth (Jainudeen et al., 1972a; Chandrasekharan et al., 1992), so offspring should theoretically benefit by inheriting traits that led to their fathers being attractive mates (Andersson, 1994) or traits associated with musth that conferred a fitness advantage (Chiyo et al., 2011b). Further experimental and observational studies are needed to elucidate the relative contribution of musth to inter- and intrasexual selection, and below we provide further reasoning and evidence for how musth may have evolved via indirect benefits models.
In polygynous systems, male reproductive success is more variable compared to females, especially when competition for mates is high (Emlen & Oring, 1977). As such, some polygynous mammals invest heavily in the survival of male offspring (Clutton-Brock et al., 1981). In African elephants, young male offspring spend more time suckling from their mothers and grow faster compared to female offspring, even though mothers produce offspring at equal sex ratios (Lee & Moss, 1986). Presumably, males that grow faster and/or larger are at an advantage when they reach sexual maturity, as entering the state of musth is dependent upon overall body condition, especially at older ages (Shannon et al., 2006b; Taylor et al., 2019). This early investment in male offspring may be especially important because mortality risk may be higher during early adulthood in males compared to females (Moss, 2001; Gough & Kerley, 2006; Wittemyer et al., 2013; LaDue et al., 2021); even though females start reproducing at younger ages and experience higher survival as a result of living in groups, males are probably capable of producing many more offspring if they survive to peak sexual maturity and continue reproducing through their lives.

Females preferentially associate with musth males, which leads to more successful mating attempts by these males (Poole, 1989b; Chelliah & Sukumar, 2015). In long-lived species with prolonged interbirth intervals, only long-term studies can answer if these intersexual associations and mating attempts lead to increased paternity success (Poole et al., 2011). Historical data and genetic analyses from a few populations in Kenya indicate that paternity levels are low among non-musth African elephant males but paternity rates increase dramatically with musth as males age, suggesting females use both musth status and age (size) in the mate selection process (Hollister-Smith et al., 2007; Rasmussen et al., 2008b). Paternity success may be complicated by factors not attributed to female choice, such as male dominance and competitive ability. For instance, most successful mating attempts for males occur among older elephants, who are also larger in size (Hollister-Smith et al., 2007; Rasmussen et al., 2008b; Keerthipriya et al., 2020). Male elephants continue to grow throughout most of their lives, and so size also is often an honest index of condition and/or dominance status with which females can assess potential mates (Sukumar et al., 1988; Shrader et al., 2006; Mumby et al., 2015). Still, the effect of size is amplified if a male is in musth; intersexual interactions occur more frequently during musth, even for smaller male elephants (Payne, 2003; Hollister-Smith et al., 2007;
Rasmussen et al., 2008b; Chelliah & Sukumar, 2013). In this context, there is growing evidence that supports an indirect benefits model of sexual selection among elephants (Figure 1).

Musth has been considered an honest signal of male condition and considered a handicap as defined by Zahavi (1975) and Zahavi (1977). However, given the continued controversy of the Handicap Principle in its varied forms (Penn & Számadó, 2020), a re-evaluation of musth in a Darwinian framework would be valuable. From musth’s first scientific descriptions, biologists have hypothesised about its value to female mate choice (Eisenberg et al., 1971; Eisenberg, 1980; Hall-Martin, 1987; Poole, 1989b), and the process of mate choice is critical for intersexual selection to occur. Sexual selection theory posits that the selection for sexual traits (such as musth) results from the balance between a mating advantage and increased risk of mortality. Male elephants in musth often forgo foraging to adopt a roving strategy — especially when they are older and larger — traveling long distances to find receptive females (Taylor et al., 2019; Keerthipriya et al., 2020; Beirne et al., 2021). Presumably, the potential fitness benefits from mating outweigh the need to find food, at least during musth. According to life-history theory, an inherent trade-off exists between foraging and reproduction. Elephants are a classic example of this, whereby males are more likely to achieve mating success the longer they stay in musth, but they must drastically reduce their time spent foraging in order to search for mates (Stearns, 1989). Therefore, females may preferentially mate with males in musth because these males are able to maintain their condition even despite their self-imposed energetic challenges. Based on all evidence collected thus far, musth is an honest indicator of a male’s condition and heightened reproductive state, so it can be reliably used by female elephants for mate assessment.

According to the Hamilton and Zuk hypothesis, another category of indirect fitness benefits proposes that sexually selected traits are indicative of resistance to pathogens, viruses, or parasites, with any resistance of successful mates being passed on to their offspring (Hamilton & Zuk, 1982). Other qualities of musth may also be inherently attractive to females; presumably a male who can sustain musth and forego foraging is also one that is relatively healthy and robust. There has been limited support for this hypothesis as it applies to musth though. For instance, although free-ranging male African elephants tend to have lower parasite loads than females, parasite load is not affected by musth status in males (Thurber et al., 2011;
Baines et al., 2015; Parker et al., 2020). Similarly, studies in Asian elephants show no intersexual differences in parasite infection rates, although parasite prevalence is relatively low in reproductively aged male elephants (Lynsdale et al., 2017, 2020). However, females may use traits other than musth (e.g., tusk length) to evaluate parasite resistance in potential mates (Watve & Sukumar, 1997). Indeed, the interplay of tusks and musth in inter- and intrasexual selection have been investigated in one population of Asian elephants (Chelliah & Sukumar, 2013, 2015), but not comprehensively in other populations of Asian elephants or at all in African elephants. The sexually dimorphic nature of tusk presence and/or length in all three elephant species perhaps allows tusks to be a reliable indicator of health and/or disease resistance (Perry, 1954; Kurt et al., 1995; Smith & Fisher, 2013). Therefore, tusks (along with other secondary sex characteristics subject to intersexual selection) may complement the multimodal musth signal for a more comprehensive process of mate choice. Additionally, it is possible that other measures will be more informative to understanding pathogen or parasite prevalence in elephant populations (e.g., hormone levels, blood pH, and urine composition), many of which would be reflected in chemical signals used for sexual selection around musth (Penn & Potts, 1998).

Besides intersexual selection, intrasexual selection/competition also can lead to the evolution of sexual traits, including multimodal signals (Andersson, 1994). Intrasexual competition contributes to sexual selection, even when potential mates are not directly assessed based on the outcomes of competition (Andersson, 1982; Andersson & Simmons, 2006). Current evidence demonstrates that musth can determine the results of competitive encounters between male elephants, even away from females (Poole, 1989b; Chelliah & Sukumar, 2013). Males rely primarily on musth as an indicator of condition and reproductive state, and physical combat between adult male elephants is rather rare, as both parties involved can experience great costs associated with fighting (Murphy et al., 2019; Keerthipriya et al., 2020). When not in musth, dominance disputes are normally resolved based on body size (and/or the presence of tusks, in Asian elephants) with larger males most often winning over smaller males (Poole, 1987; Chelliah & Sukumar, 2013, 2015). However, musth status is the most important determinant of dominance among males, even in spite of any counteracting size influences (Poole, 1989a, b; Chelliah & Sukumar, 2013; Wyse et al., 2017). In other words, even a smaller male in musth can exclude a much larger non-musth
male from gaining access to females using various signals (Rasmussen & Krishnamurthy, 2000; Rasmussen et al., 2002; Greenwood et al., 2005), potentially even at extreme size discrepancies (de Silva et al., 2014).

In African elephants, evidence suggests that younger males are suppressed from entering musth by the presence of older, musth males (Poole, 1989a; Slotow et al., 2000; Murphy et al., 2019). While the mechanism of physiological suppression in male elephants is unclear, it could be a combination of chemical or behavioural signals, physical combat, the simple presence of dominant animals, and/or mate choice, as has been observed in other vertebrates (Young, 2009); reproductive suppression is observed in some socially and cooperatively breeding mammals as a form of competitive exclusion stimulated by female mate choice (Clutton-Brock, 2009). Furthermore, male–male competition for access to mates is especially high for African elephants in some habitats; older males may enter musth during rainy seasons when resources (potentially both food and water) are more abundant, and they stay in musth for longer periods (Hanks, 1969; Poole, 1987). These older males forgo musth when environmental conditions are unfavourable — or when females leave an area to follow the rains — and younger males may exhibit musth episodes that are shortened by environmental and social pressures (Poole et al., 2011). Alternatively, young males may be forced to be more selective and enter musth only when in proximity to females they assess to be receptive (e.g., through pheromones in female urine). Both of these scenarios bolster the argument of musth’s utility in intrasexual competition.

Indirect benefit models illustrate the flexibility of sexual selection across a range of species. For elephants, these indirect benefits are conferred via mate choice and intrasexual competition simultaneously. A female elephant can enhance her offspring’s fitness by preferentially mating with musth males, especially if this preference is widespread in a population, and any resulting male offspring should be genetically predisposed to sustain musth with good health even during periods of fasting. In turn, this investment helps ensure that male offspring are both capable mates and competitors.

5. Future research

Despite the evidence presented here, we still have much to learn about musth and sexual selection in elephants. After all, body size and health condition
should be sufficient indices of a male’s reproductive ability in most cases, but the existence of musth itself — and its role as the predominant male mating strategy among all three elephant species — suggests that its evolutionary benefit(s) outweigh(s) any other costs. We already have discussed several topics related to musth that need investigation. In summary, these include that the multiple sensory components of the musth signal (visual, acoustic, and chemical) deserve further attention, such as: (1) the relevance of each component between various spatial and temporal scales, (2) the forces that shape these signals during musth, (3) the possibility that signal component(s) exist on a gradient to reflect the progression of musth, and (4) how (or if) these components interact to communicate musth. Further, while there is evidence that supports the role of musth in both inter- and intrasexual selection, more studies are warranted that test hypotheses related to these concepts. This future research will better elucidate the relative contribution of musth to processes like female mate choice and male–male competition, which may change with properties of the male and his social and/or physical environment.

Along with these areas of future research, other concepts are left to explore about musth and its significance as a classic example of sexual selection. One aspect of sexual selection that is not well understood in most mammals is postcopulatory selection, such as sperm competition and cryptic female choice. Sperm competition, a form of intrasexual competition whereby sperm cells compete for the ability to fertilise available ova, is prevalent in many mating systems, including seasonally breeding ungulates (Parker, 1970; Dixson & Anderson, 2004; Martinez-Pastor et al., 2005; Eberhard, 2009). In mammals, this process has led to variation in sperm morphology, male reproductive structures, and associated secondary sexual characteristics (Gomendio & Roldan, 1991; Malo et al., 2005; Tourmente et al., 2011). One explanation — the phenotype-linked fertility hypothesis — posits that male secondary sexual characteristics are honest indices of the quality of a male’s ejaculate (Sheldon, 1994). If this is the case in elephants, then musth could be a signal of sperm quality; we simply do not know how likely these similar systems are to occur in elephants.

We have provided evidence that males may enter musth in part as a mate-guarding strategy via intrasexual competition (Poole, 1989b; Chelliah & Sukumar, 2013; Keerthipriya et al., 2020). If mate guarding is successful,
males may effectively circumvent the need for sperm competition; the presence of a musth male would cause non-musth males to leave the area, and if females are in oestrus, the musth male could successfully monopolise copulations. However, musth males may not be able to control access to oestrous females, and so sperm competition may increase the likelihood of paternity with musth. Musth is characterised by elevated androgen levels, which may serve to promote sperm production, as observed in other mammals (Dixson & Anderson, 2004; Minter & DeLiberto, 2008; Malo et al., 2009). However, no comprehensive studies have been published that directly investigate the influence of musth on male reproductive function and/or semen/sperm quantity or quality; it is not currently possible to evaluate whether postcopulatory sexual selection influences musth because the process of collecting semen from a male elephant in musth is difficult (Howard et al., 1984; Schmitt & Hildebrandt, 1998). Anecdotally, evidence suggests optimal semen quality is often observed in bulls a few weeks prior to musth, perhaps indicating semen quality is enhanced as androgen levels begin to increase during pre-musth periods (Kiso, personal observation). We know that captive male elephants regularly produce viable sperm and breed frequently with receptive females regardless of their musth status (Kiso et al., 2007; Brown, 2014), and at least some offspring in wild elephants are sired by non-musth males (Hollister-Smith et al., 2007; Rasmussen et al., 2008b). In light of this, the question remains as to whether musth males have a reproductive advantage due to postcopulatory selection. Perhaps increased progress in assisted reproductive technologies will make it more efficient to assess semen quality and reproductive function in ways that have previously been unachievable, thereby indicating if and how sperm competition related to musth occurs in elephants (Hildebrandt et al., 2000).

Evidence of successful fertilization outside of musth in African elephants also supports the possibility of other reproductive dynamics in elephants such as cryptic female choice (Hollister-Smith et al., 2007; Rasmussen et al., 2008b). Cryptic female choice refers to any physical or chemical process whereby females mate with multiple males and manipulate which sperm fertilise available ova after copulation has begun and/or ended (Eberhard, 1996, 2009). Male elephants — even smaller males not in musth — hypothetically should be able to coerce a female to copulate by physical strength alone (although in African elephants, copulation often causes excitement among female conspecifics that may discourage unsolicited mating attempts; Moss,
Even though musth males appear to monopolize access to ovulating females, this is probably impossible to do. Therefore, female elephants may copulate with multiple males (Poole et al., 2011); however, no research to date has examined whether female elephants practice postcopulatory mate choice.

Two related possibilities — the immunocompetence handicap hypothesis and the challenge hypothesis — explain why males with heightened androgen concentrations (i.e., those in musth) are most successful in securing mating opportunities, as increased testosterone associated with musth may also suppress immune function. The immunocompetence handicap hypothesis (Folstad & Karter, 1992) — not to be understood as a handicap hypothesis by Zahavi (1977) (Penn & Számadó, 2020) — suggests that only males that can afford poor immunocompetence can produce larger amounts of testosterone due to reduced immune function and/or higher rates of parasite infection (Saino et al., 1995; Verhulst et al., 1999; Hughes & Randolph, 2001). If this is the case in elephants, immunocompetence may strengthen musth’s honesty as a signal to females. Yet, even though a variety of parasites and infectious pathogens may cause disease in wild populations (Fowler, 2006), this phenomenon has not been studied in elephants. In conjunction with the immunocompetence handicap hypothesis, the challenge hypothesis posits that androgen levels are high to prepare for male–male competition and aggression during times when the probability for copulation is high (Wingfield et al., 1990). If this applies to elephants, then the costs of a compromised immune system and concomitant energetic demands for mate defence during musth should only be justified when the chance to mate with female(s) is relatively high. The challenge hypothesis enjoys empirical and observational support in a variety of vertebrates (Hau et al., 2004; Muller & Wrangham, 2004; Girard-Buttoz et al., 2015; Maney, 2020), and so it may be present in elephants too.

Many of these hypotheses would be difficult to study in large, long-lived animals like elephants in their natural setting. However, the careful research of captive elephants has revealed much about the mechanisms behind communication and reproduction that continue to inform and contextualise field studies in these species (Bechert et al., 2019; LaDue, 2019). Indeed, musth was first described in ancient times among captive elephants in Asia (Spinage, 1994), and reports of the behavioural and physiological correlates of musth in captive elephants abound in the literature (Jainudeen 1983).
et al., 1972b; Hromadka, 1986; Niemuller-Hare et al., 1988; Brannian et al., 1989; Cooper et al., 1990; Lincoln & Ratnasooriya, 1996; Flora et al., 2003; Ganswindt et al., 2005a; Scott & Rasmussen, 2005; Brown et al., 2007; Hollister-Smith et al., 2008; Santiapillai et al., 2011; Duer et al., 2016; Chave et al., 2019). Musth is prevalent among captive male elephants, with significant variation in duration, frequency, and intensity (Scott & Riddle, 2003; LaDue et al., 2014). Because the physical and social environments are different in captivity from those of wild elephants, we strongly suspect that musth is plastic and sensitive to both intrinsic and extrinsic factors. For example, captive male elephants can undergo acute musth episodes, longer than what is typically observed in wild elephants (LaDue et al., 2014), perhaps resulting from the enhanced nutrition and veterinary care associated with captive environments and/or more frequent or prolonged contact with conspecifics in close proximity. It would be reasonable that similar musth dynamics occur in wild populations, offering additional opportunities to study inter- and intrasexual selection related to musth in elephants. Similarly, many of the potential explanations we have introduced and discussed here as deserving of further attention may only be researched among captive elephants. These studies potentially complement — but do not replace — data from wild populations, lending insight into how sexual selection occurs in these fascinating and complex species.

6. Conclusion

Sexual selection continues to be vital for understanding communication and reproductive behaviour in animals (Eberhard, 2009; Jones & Ratterman, 2009), even 150 years since Darwin first described his theory in ‘Descent of Man’ (1871). Elephants provide ample opportunity to observe sexual selection in a long-lived, socially complex mammal (Figure 1). The phenomenon of musth is inextricably linked to sexual selection in elephants; it is observed in all three species and facilitates both intersexual selection and intrasexual competition. Unlike in other seasonally breeding mammals that exhibit rut or rut-like behaviours during a specific period, musth is asynchronous and occurs throughout the year as does potential female receptivity. Male elephants appear to use musth as a multimodal signal — comprised of visual, acoustic, and chemical components — to convey intent to conspecifics of both sexes. Nevertheless, further work is needed to understand the signal
value of each modality and the form of their interaction(s). The importance of musth as a reproductive strategy also deserves further investigation to understand its adaptive value. Compared to non-musth males, males in musth seem to have inordinate access to breeding opportunities that are relatively rare, and males in musth successfully dominate potential non-musth competitors even in the presence of other signs of superior status (e.g., body size). Evidence points to the value of indirect benefits female elephants can gain from mating with musth males, but there is still much to learn from the female perspective in terms of postcopulatory selection and cryptic female choice. This should begin with a better understanding of how and why musth makes male elephants better mates and competitors. Ongoing and future studies of male elephants and their behaviour promise new insights that will better contextualise musth as a sexually selected, multimodal signal and solidify it as a classic case of sexual selection.

Acknowledgements

We appreciate the conversations with elephant professionals around the world that helped to inspire this work. We also thank anonymous reviewers whose perspectives improved this manuscript. Fieldwork leading to ideas presented in this manuscript was supported by the Animal Behavior Society, Asian Elephant Support, American Society of Mammalogists, Cosmos Club Foundation, Earthwatch Institute, Elephant Managers Association, Explorers Club, Feld Entertainment Inc., IDEA WILD, International Elephant Foundation, George Mason University (Department of Biology, Office of the Provost, School of Integrative Studies), National Geographic Society, National Science Foundation, Oklahoma City Zoo Conservation Action Now, Saint Louis Zoo WildCare Institute, US Fulbright Student Program (US–Sri Lanka Fulbright Commission), Virginia Academy of Science, and Western Kentucky University (Advanced Materials Institute, Biotechnology Center, Center for Biodiversity Studies, Department of Biology, Graduate School).

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