

Dance displays in gibbons: Biological and Linguistic perspectives

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Abstract

Female crested gibbons (genus *Nomascus*) are known to perform stereotyped sequences of jerking movements, involving the rump and extremities. These dances have attracted little scientific attention and thus their structure and meaning remain largely obscure. We analysed close-range video recordings of captive crested gibbons to extract detailed descriptions of dance in four *Nomascus* species (*N. annamensis*, *N. gabriellae*, *N. leucogenys*, & *N. siki*). We report results from a survey among relevant professionals clarifying behavioural contexts of dance in captive and wild crested gibbons. Our results demonstrate that dances in *Nomascus* represent a common and intentional form of visual communication restricted to sexually mature females. While primarily used as a proceptive signal to solicit copulation, dance occurs in a wide range of contexts related to arousal and/or frustration in captivity. A linguistically informed view of this complex sequential behaviour demonstrates that gibbon dances can follow a nested grouping organisation – a pattern so far not described for visual displays in other non-human primates. We propose that crested gibbon dances likely evolved from less elaborate rhythmic proceptive signals, such as those found in siamangs and hoolock gibbons. Although dance displays in humans and crested gibbons share a number of key characteristics, they cannot be assumed to be homologous. Nevertheless, gibbon dances represent a valuable model behaviour to study the utilisation of complex gestural signals in hominoid primates.

Key words: Dance syntax, primate communication, Super Linguistics, small apes

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1. INTRODUCTION

The concept of *dance* is primarily discussed in the context of human communication, where dancing is defined as intentional, rhythmic and non-mechanically effective body movements (see e.g. Hanna 1979, 2017). However, this definition can also be applied to certain social behaviours in other animals, including primates, whose (potential) dance displays have only received limited attention so far (Francis 1991; Fan et al. 2016 for gibbon dances; Bertolo et al. 2021 for chimpanzee rhythmic displays). Indeed, it overlaps with that of a communicative *gesture* in non-human primates, typically defined as a discrete, intentional movement of a body part, which is potentially detectable by an audience and non-mechanically effective (Genty et al. 2009). Notably, dance is broader, in that it includes non-discrete movements and ‘global’ movements of the entire body, and definitions of gesture generally lack the rhythmic component central to common definitions of dance (as in the anthropological work of Hanna 1979, 2017). Criteria used to assess intentionality in animal gestures and dance (inherent to both definitions) vary between studies but usually include sensitivity to the presence or attentional state of an audience, persistence and/or elaboration until the emitter’s goal is reached (Cartmill and Byrne 2010; Genty et al. 2009).

Here we focus on an understudied form of visual communication that is characteristic to adult female small apes of the genus *Nomascus*, commonly referred to as crested gibbons. Our approach relies on the joint efforts of linguists and biologists, aiming to characterise complex animal communication signals via means of both biological and linguistics tools (i.e. see Berthet et al. 2023). The visual display studied here takes the shape of rhythmic intentional movements of the entire body, thus qualifying as dance, and as different from gesture.

Gibbons are exclusively arboreal apes (superfamily *Hominoidea*) that live in small territorial social units, typically structured around a single monogamous breeding pair (Malone and

Fuentes 2009). With regards to social communication, investigations have largely focused on their vocal behaviour, which include highly elaborate song bouts (Clarke et al. 2006; Geissmann 2002). *Nomascus* represents one of four extant gibbon genera (Mootnick and Fan, 2011). Taxonomists distinguish seven *Nomascus* species, which occur in the tropical and temperate forests of Southern China, Eastern Indochina and the island of Hainan (Mootnick and Fan 2011; Roos 2016). All of these species are sexually dichromatic, with dark pelage colour in males and light colouration in females, and exhibit striking ontogenetic colour change (Mootnick and Fan 2011). At the behavioural level, *Nomascus* differ from other small apes in the frequent occurrence of polygynous rather than monogamous groups in wild populations (Delacour 1933; Guan et al. 2018; Li et al. 2022). However, polygynous habits have so far mostly been reported from northern *Nomascus* species (*N. concolor*, *N. hainanus*, *N. nasutus*), while the more limited number of studies on the socioecology of the southern species group (*N. annamensis*, *N. gabriellae*, *N. leucogenys*, *N. siki*) suggest polygyny to be rather exceptional (Barca et al. 2016; Hong-Wei and De-hua 1989; Kenyon et al. 2011). The diversity and usage of facial expressions in crested gibbons is similar to that of other hylobatids (Florkiewicz et al. 2018; Scheider et al. 2016); their gestural repertoire has never been comparatively assessed in a rigorous manner (but see De Vries, 2004).

Dances in crested gibbons were first noted anecdotally in captive individuals (Maxwell 1984). Lukas et al. (2002) were the first to systematically monitor the occurrence of such displays (therein described as “bobbing”), remarking that their frequency increased during oestrus in the single mated Northern white-cheeked gibbon (*N. leucogenys*) female that they studied. Subsequent observations on wild crested gibbons support the assumption that the dances function primarily as proceptive signals to solicit copulation and are only displayed by adult females (Fan et al. 2016; Li et al. 2022; Zhou et al. 2008). During a dance, the gibbons do not vocalise (Fan et al. 2016).

To date, the most comprehensive analysis of this behaviour has been provided by Fan et al. (2016), who report the occurrence of dances in four wild adult females of the Eastern black crested gibbon (*N. nasutus*). They characterise the female display in terms of “a rhythmic moving of her body (arms, legs, trunk, and head) [...] while maintaining other body parts motionless [...] similar to a human ‘Robot Dance’” (Fan et al. 2016). They offer observations of the contexts in which dances occur and also provide descriptions of the structure of two selected dancing bouts. Finally, they noted the subsequent behaviour of associated males, who responded positively (approach, grooming or copulation) to 46.2% of dancing bouts (112 of 242 instances). Fan et al. (2016) hypothesise that dancing serves several functions: besides soliciting copulation, it may also strengthen inter-sexual social bonds and could represent a form of non-aggressive intrasexual competition between females within polygynous groups. However, although *Nomascus* dances are frequently observed in both wild and captive settings (Burns and Judge 2015; De Vries, 2004; Fan et al. 2016; Lukas et al. 2002; pers. obs.), neither rigorous tests of these hypotheses nor detailed analyses on the phylogeny, structure, and variability of dances have been conducted.

Addressing part of the aforementioned knowledge gaps, we analysed close-range video recordings of captive crested gibbons to provide novel descriptions of dance in females from four *Nomascus* species (*Nomascus annamensis*, *N. gabriellae*, *N. leucogenys* and *N. siki*). In addition, we report the results from a survey among professionals (see Methods section) on the occurrence and context of dance displays in captive as well as wild crested gibbons. Based on our findings, we developed a linguistically informed view of this complex sequential behaviour.

2. MATERIALS AND METHODS

2.1 DATA COLLECTION AND DEFINITION OF GIBBON DANCE

In total, we compiled 37 videos capturing behavioural sequences including a dance event, of which 11 were discarded from all subsequent analyses due to external disturbances (e.g. a human approaching/interacting directly with the animal). The 26 remaining videos were used for the intentionality analysis. Seven videos were further discarded from the grouping analysis due to limited visibility preventing a fine-grained analysis of movement patterns. The videos were opportunistically recorded from 11 captive *Nomascus* females housed in European and Australian zoos (Table 1), as well as in the Endangered Primate Rescue Center (EPRC Vietnam). Information about the identity and origin of each subject in the video analysis are summarised in Table 1. Video material was either derived from the personal archives of the authors or was solicited from researchers and zoo staff via the research survey accompanying this study.

We defined dance as an abrupt temporary stiffening of the body accompanied by rhythmic, often repetitive jerky body movements (e.g. stereotyped movement of the rump and/or the limbs and head). Movements that did not fit this definition but appeared within a dance sequence (self-scratching; locomotion) were excluded from the analyses. In the vast majority of dance sequences, the dancing female's back was turned towards the recipient, but apart from this generalisation, dance structure was highly variable (see results).

Table 1: Information on subjects and dance sequences considered for analyses on intentionality and grouping (EPRC: Endangered Primate Rescue Center, Cúc Phuong, Vietnam). The column “total number of dances” equals the number of dances considered for the intentionality analysis.

Species	Individual	Location	Age in years at recording	total # of dances	# of dances in grouping analysis
<i>Nomascus annamensis</i>	Hu (TJD21-00751)	EPRC	~9 (wildborn)	7	7
<i>Nomascus gabriellae</i>	Ina (TJD19-00500)	EPRC	22	9	8
<i>Nomascus leucogenys</i>	Chukhao (MIG12-28443496)	Parc Zoologique & Botanique Mulhouse	10	1	0
	Lucki (MIG12-29370588)	Zoo Duisburg	7	4	0
	Polly (TJD19-00461)	EPRC	~14 (wildborn)	1	0
	Jermei (MIG12-29965298)	Perth Zoo	21	1	1
<i>Nomascus siki</i>	Doremon (TJD19-00497)	EPRC	~7 (wildborn)	2	2
	Hope (TJD19-00491)	EPRC	11	1	1

2.2 ASSESSMENT OF INTENTIONALITY

We used standard criteria from great ape research to assess intentionality (Cartmill and Byrne 2010; Genty et al. 2009): sensitivity to the attentional state of the audience (assessed via measures of audience checking and attention-getting behaviours), persistence (i.e. pursuit of the behaviour after audience checking) and elaboration (i.e. inclusion of novel behaviours to the dance). The presence or absence of each of these behaviours was assessed by an experienced coder (CC) and scored as a binary variable for each dance bout. All cases in which the applicability of these concepts was deemed to be even slightly ambiguous have been coded as negative, thus leading to a highly conservative assessment. An audience (conspecific and/or heterospecific) was present and able to see the dancing female in each of

the 26 videos analysed. A potential caveat is that more than half of the dances were recorded by an experimenter holding a camera in close proximity to the gibbon, thus making the presence of an attentive audience (i.e. an individual oriented towards the female) a prerequisite for the acquisition of the footage. This is one of the reasons why a more fine-tuned criterion to assess audience sensitivity (i.e. audience checking) was adopted.

2.3 ASSESSMENT OF STRUCTURAL GROUPING

We qualitatively analysed the structure of the dancing bouts in terms of *grouping*. Analogous to research on human dance (Charnavel, 2019), groups were defined as homogeneous, continuous behavioural sequences which constitute unitary blocks within the dance bout. Grouping gives rise to a (rudimentary) syntax, i.e., a system of possible movement sequences that is plausibly governed by rules that generate well-formed and ill-formed sequences (compare Berthet et al. 2023).

Groupings of movement patterns in the gibbons' displays were assessed by a trained linguist (PPG), with extensive experience in human dance cognition. In addition to the subject's posture (i.e. sitting, standing, hanging or crouching), selected behavioural variables were coded systematically (Table 2) and used to define groups of movements and group boundaries within a display bout.

Table 2: Behavioural variables included in the grouping analysis and their definition

Behavioural category	Variable	Definition
Global body movement	Up-down	Repeated vertical movement of the body
	Left-right	Repeated lateral shifting of the body
	Diagonal	Repeated diagonal movements of the body (i.e. the direction cannot be coded as purely vertical or horizontal)
	Alternating	Alternation of vertical, horizontal and diagonal movements with no clear repetition pattern of a given direction
	Front-back	Repeated body movement from front to back, with no vertical or lateral component
	Body shake	Stereotyped shaking of the entire body (similar to a gibbon's movement to rid its coat of water – Baldwin & Teleki, 1976)
Movement of discrete body parts (limbs or head)	Head movement	The individual turns its head to either side
	Arm extension	The individual extends an arm away from the body *

* This behavioural item does not include begging, which we define as “sustained extension of an arm in the direction of a human observer, with clear eye contact”

2.4 RESEARCH SURVEY

We conducted a self-administered online survey (via Google Forms) which was disseminated by email to relevant professionals with expertise in crested gibbon behaviour (field primatologists and zoo staff, including curators, veterinarians and primate keepers). The distribution of the survey was supported and facilitated by the Gibbon Taxon advisory group (TAG) of the European Association of Zoos and Aquaria (EAZA) and the Gibbon Species Survival Plan® (SSP) steering committee of the Association of Zoos and Aquariums (AZA) after a careful evaluation of the project. The survey was made available between November 2022 and June 2023. It included 12 questions (Suppl. File 1), pertaining to the occurrence of

dance, the sex, age and contraceptive status (i.e., with or without hormonal contraception) of the dancing individuals, the behavioural context of dances, and the professional background and experience of the respondent. The survey contained an exemplary video of a dance (Suppl. File 2) showcasing what type of behaviour the study dealt with. We received 27 responses to the survey.

3. RESULTS

3.1 INTENTIONALITY

We found dance in *Nomascus* to comply with criteria of intentional communication. In 61% of dances (i.e. 16 instances), a clear audience-checking behaviour during the dance could be identified (in 13 cases i.e. 50%, that behaviour was repeated several times during the dance bout). We identified 4 instances in which the female displayed attention-getting behaviours (3 instances in which the female repositioned herself in space to be in front of the receiver after she moved, and one hand slapping behaviour). Persistence after audience checking occurred in 57% of the dances (i.e. 15 dances). Finally, we found several cases (from two females) which could reflect elaboration: the females extended their arm in a begging gesture immediately after they stopped dancing. This behaviour needs to be interpreted carefully, as the contextual information available does not allow us to confirm that the female's initial goal was to obtain food from the human towards whom the dance was directed.

3.2 GROUPING

The 19 dances analysed for grouping structure had a mean duration of 20 s (+/- 23, range: 6 – 126s). Multiple groups were identified in 13 out of 19 videos analysed. Two main changes in gibbon dance sequences were observed that plausibly give rise to grouping boundaries (*Grouping Preference Rules, GPRs*), namely *change of contact point with the*

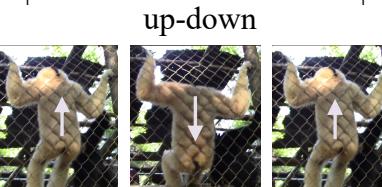
substrate/weight shift (Charnavel's GPR3) and *change of direction* (GPR4), as defined in Charnavel (2019). To elaborate, in GPR3, the contact point with the substrate changes (e.g. between sitting and standing) while the direction stays constant (e.g., left-to-right), a change in human dance sequences that would give rise to the perception of grouping boundaries. Similarly, a change from left-right movement to repeated rhythmic up-down movement would correspond to *change of direction* (GPR4), as the movements differ in the direction of their respective path. It is unclear whether these two rules are weighted differently when both create grouping boundaries in a given dance sequence.

We recognise a spectrum of complexity in gibbon dances. Within it, we identify three main types of grouping structures: homogeneous dances ($n = 6$), where the dance consisted of a single group (Suppl. File 3); simple dances ($n = 9$), where we identified groups within the dance but no nested structure (Suppl. File 4); and complex dances ($n = 4$), i.e. in which smaller (lower-level) groups were nested within larger (higher-level) groups (Suppl. File 2). Homogeneous dances (Fig. 1a) were expressed as rhythmic twitches or bobbing movements of the whole body and occurred without the sequential changes in posture seen in simple and complex dances. Simple dances (Fig. 1b) contained 4.4 groups on average (+/- 1.3), while complex dances (Fig. 1c) counted 4.5 higher-level groups (+/- 2.5) and 7.25 lower-level groups (+/-1.7; average number of lower-level groups per higher-level group).

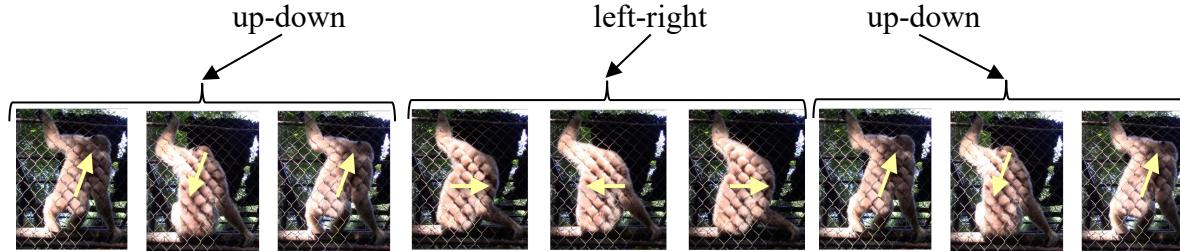
Posture (change of contact point with the substrate; GPR3) and direction of (jerky) movement (GPR4) appeared to be key in setting (both higher-level and lower-level) group boundaries. In one nested dance GPR3 was marking strong group boundaries, GPR4 marked those in two nested dances and in one case both GPR3 and GPR4 marked strong group boundaries. Interestingly, the behavioural category setting the higher-level vs lower-level boundaries

could change between dances, even within an individual. For instance, in some of Ina's (*Nomascus gabriellae*, Endangered Primate Rescue Centre, see Table 1) dance sequences, posture set the higher-level group boundaries while direction of movement set the lower-level ones, and in other dance sequences it was the contrary.

Grouping by direction |-----| (a)



Grouping by direction |-----|-----| (b)



sitting

(n/a)

sitting

standing

sitting

standing

(c)

Grouping by posture: |-----|

Grouping by direction |-----|

left-right

up-down

left-right



Fig. 1 Schematic representation of movements in (a) homogeneous dances, (b) simple dances and (c) complex dances. In the latter, postures are marked with colours. Note the alternation of non-nested left-right and up-down movements the first half, followed by left-right movements nesting in alternating sitting and standing postures

3.3 RESEARCH SURVEY

We received 27 responses from representatives of 26 institutions to the self-administered survey on crested gibbon dance. Of these, 25 responses came from zoos and rescue centers in Europe, the United States, and Vietnam, and two from researchers studying gibbons in their natural habitats. Respondents, were animal caretakers (51.9 %), scientific staff (curators / researchers, 25.9%), veterinarians (7.4%), and 4 persons who reported to represent neither of the mentioned professions but extensive experience with *Nomascus* gibbons (14.8%). Respondents' experience with gibbons varied between "several months" and 39 years. The respondents with at least one year of experience with small apes (n = 26), had worked with these primates for 9.7 ± 8.6 years on average.

The respondents observed a total of 136 captive gibbons (*N. annamensis* (1 institution), *N. gabriellae* (6 institutions), *N. leucogenys* (18 institutions), *N. siki* (1 institution)) as well as 8 wild gibbon groups (*N. concolor* - 4 family groups, Xiaobahe, Wuliang Mountains, Yunnan, China; *N. nasutus* - 4 family groups, Trung Khan District, Vietnam). Within this extensive sample, 16 respondents (59%) have observed dances, which occurred in all covered species except for *N. concolor*, while 11 (41 %) reported to have never noticed this behaviour. Dancing individuals were exclusively female.

Nomascus females of all age classes (see Suppl. File 1), except for the youngest (0-3 years) were observed to dance. However, older juveniles and young subadults (3 – 5 years) were only observed to dance by two respondents (6%), with one specifying that dance behaviour onset at an age of 4 years. Dance was still observed in females older than 35 years (4 respondents, 13%) and is therefore present in senescent individuals.

Observed dances were not just targeted towards other gibbons (12 responses, 75% of positive responses), but even more so towards humans (13 responses; 81% of positive responses). Three respondents even reported to have only observed human-targeted dances (19% of

positive responses). Only one out of all respondents working with captive gibbons communicated that dances were restricted to conspecific communication. Finally, one respondent noted observed dances were also directed towards primates that were neither gibbons nor humans (a situation we observed as well in the female “Lucki” from Duisburg zoo) and three of the surveyed reported to have seen dances that were not targeted towards a conspecific or heterospecific receiver, possibly representing displacement behaviour.

Gibbon-directed dances were primarily observed in the context of copulation (9 responses, 75% of responses reporting dance targeted at conspecifics) and socialisation / grooming (4 responses, 33%) and to some extent also in stressful situations (2 responses, 17%) or in feeding contexts (1 response, 8%). Human directed dances were most frequently reported from situations involving interspecific socialisation and grooming (9 responses, 69% of responses reporting dance targeted at humans), and contexts of disturbances (5 responses, 38%; possibly displacement actions) as well as feeding (4 responses, 31%). The latter include dances apparently performed in anticipation of receiving food. Analogous to that, one of the respondents reporting dance targeted at humans (8%) reported that dances occurred before commencing a training session. Three respondents (23%) interpreted dances directed towards humans as sexual solicitations. No respondent noticed effects of hormonal contraception on dance behaviour.

Ultimately, three out of all 27 respondents (11%) noted that they have observed behaviours similar to crested gibbon dances in female siamangs.

4. DISCUSSION

4.1 GENERAL DISCUSSION

Our data and accompanying survey demonstrate that dance is a common social display in gibbons of the genus *Nomascus*, also occurring in species so far not reported to exhibit dancing (*N. annamensis*, *N. gabriellae*, *N. siki*), and lacking polygynous mating systems to notable extents (e.g., Barca et al. 2016; Hong-Wei and De-hua 1989; Kenyon et al. 2011; see Fig. 2). The only *Nomascus* species for which observations of dances are now lacking, is the Western black crested gibbon (*N. concolor*). This species is not housed in captivity but has been subject to long-term field studies (Hu et al. 2018). While detailed accounts of its mating behaviour have been published, they do not mention female dances of any form (Huang et al. 2013; Zheng 1988). However, given that this peculiar behaviour has long escaped scientific attention in other *Nomascus* species, it certainly appears possible that it will be described in *N. concolor* eventually.

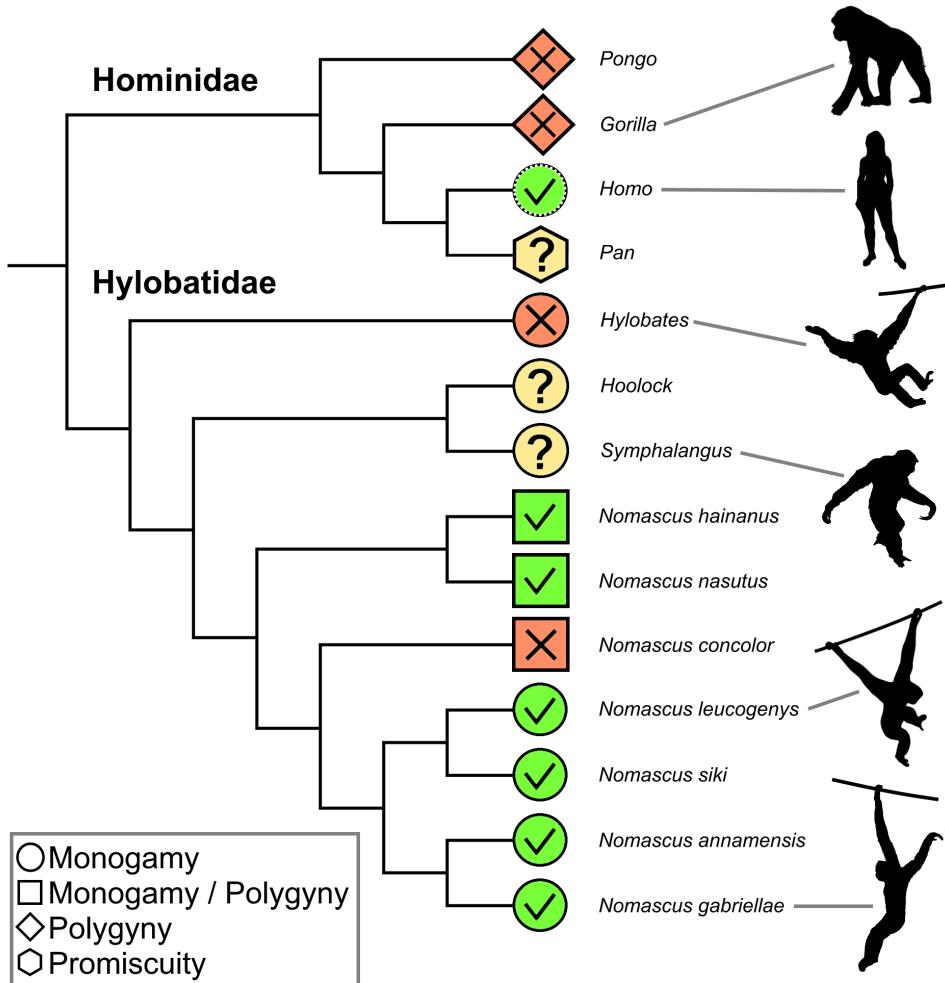


Fig. 2 The occurrence of dance in social communication and mating systems across apes (superfamily *Hominoidea*). Colours and symbols denote the presence (green tick) or absence (red cross) of dancing based on current evidence. The genera *Hoolock*, *Pan*, and *Sympalangus* show rhythmic displays that may qualify as dance but are insufficiently characterised at the moment (yellow question mark). The original human mating system is tentatively hypothesised as a type of monogamy here. Mating systems are defined as: monogamy – both sexes mate primarily with one partner; polygyny: males have typically at least two (or multiple) female partners, while females have primarily one male partner; promiscuity – both sexes mate with multiple partners. Hylobatid tree topology follows Shi & Yang, 2018 and Thinh et al. 2010

Our data support the notion that only sexually mature female crested gibbons perform dances, but also that dancing is still present in female individuals of advanced age that may no longer be reproductively active. Survey results suggests that the onset of dance behaviour falls

within the time window of menarche (4.6 – 7.7 years – Bolechova et al. 2019; Margulis and Hálfdanardóttir 2021) and the subsequent development of an adult pelage colouration in captive *Nomascus* (5 – 8 years; Geissmann et al. 2000), however future studies are required to confirm a correlation of dance onset and these ontogenetic events at the individual level. Furthermore, our findings show that dances in *Nomascus* represent a form of intentional communication, as do visual gestures previously described for great as well as small apes (e.g., Byrne et al. 2017; Liebal et al. 2004). While our survey results confirm that dances act as proceptive signals that solicit copulation (Fan et al. 2016; Li et al. 2022; Lukas et al. 2002; Zhou et al. 2008), they also occur in a number of different behavioural contexts relating to non-sexual arousal, at least in zoo-housed gibbons, and regardless of whether a female is experiencing oestrus or is contracepted (although the frequency of dances in general could be affected by the oestrus cycle – Lukas et al. 2002). Future research needs to clarify whether dancing in certain circumstances is specific to captive gibbons. In orang-utans, for instance, it has previously been shown that gesture use can differ markedly between wild and captive populations (Fröhlich et al. 2021).

Our finding that captive female crested gibbons often direct dances towards human keepers prior to feeding or during social interactions suggests that they can act in non-sexual attention-getting, as originally suggested by Maxwell (1984) and later hypothesised by Fan et al. (2016) (see Caspar et al. 2020 for further discussion on attention-getting in captive gibbons). Alternatively, rather than being goal-directed, dances may simply allow females to relieve tension in context of arousal or frustration (see Botting and Bastian 2019). However, given the intentional dimensions and complex structures of the dances that we described here, the first option appears more plausible. In any case, frustration paired with excitement may be cross-context drivers of dancing. Indeed, stereotyped body-shaking, which is incorporated

into 6 dances (32%), has previously been described as a frustration-related behaviour in gibbons (e.g., Baldwin and Teleki 1976; Maxwell 1984).

Different from any visual gesture known from other non-human primates to date, *Nomascus* dances can display variable grouping structures. Two or more structural groups could be identified in 71% of the dance displays analysed. It remains to be seen if, and how grouped dances differ from homogeneous dances with regards to their meaning. Notably, we identified sequences of nested groups, as proposed in linguistic approaches to other cognitively complex behaviours. Previous work has reported hierarchical structures in the vocal communication of birds (Berwick et al. 2011) and orangutans (Lameira et al. 2023). Based on the sample size, data collection methods and contexts, it remains unclear whether gibbon dances consist of compositional semantic contents, or iconic components. Interestingly, other complex visual displays exist in non-primate animals, which may also bear a potential hierarchical structure. This is for instance the case of the courtship displays of some birds-of-paradise species of the genus *Astrapia* (Aves: *Paradisaeidae*) in which one movement pattern, the “flick-pivot” motif, involves repeated wing flicks displayed while the male moves side-to-side in space (Scholes et al. 2017).

4.2 PHYLOGENETIC PERSPECTIVES

Because dances, at least in wild crested gibbons, most obviously function in soliciting copulation (Fan et al. 2016; Li et al. 2022; Zhou et al. 2008), they likely evolved as a proceptive gesture. Hence, proceptive displays in other gibbons might provide clues about the evolution of dance behaviour in gibbons. Nothing resembling a dance is known from dwarf gibbon social communication (genus *Hylobates*; see e.g., Baldwin and Teleki 1976; Palombit 1992; but note dance-like decoy displays in wild Kloss gibbons (*Hylobates klossii*) – Dooley and Judge 2015). However, female siamangs (genus *Sympalangus*) and hoolock gibbons

(genus *Hoolock*) have been reported to also use rhythmic body movements to invite their partners to mate; this is particularly well known in siamangs and often accompanied by another conspicuous signal, a quick throw-back of the head (Liebal et al. 2004). It is characterised by jerking movements of the upper body mediated by repeated angling and stretching of the arms and has been observed both in the wild (“upward-thrust” – Palombit 1992) and in captivity (“jerking body movements” – Liebal et al. 2004; Orgeldinger 1999). This display appears to be very similar to simple dances in *Nomascus* and three respondents to our survey actually reported having observed “dances” in siamangs. As in *Nomascus*, siamangs’ jerking body movements can be flexibly performed with regards to posture and may occur while the female is either suspended or sitting (Liebal et al. 2004). Different from the former, however, no conspicuous movement of the limbs independent of the body nor sequential changes in posture were reported to occur, and no information on the length of the displays is available. In adult siamangs, jerking movements have also not been reported outside of sexual contexts, so far, and different from *Nomascus*, juvenile siamangs use them to initiate play (Liebal et al. 2004).

For wild Eastern hoolock gibbons (*Hoolock leuconedys*) “head nodding” (which might potentially be equivalent to the “throw-back head” signal in siamangs) and branch shaking, have been described as female gestures to solicit mating (Kumar and Sharma 2017). Nevertheless, via our survey, we received a short video of a female Eastern hoolock housed at the Gibbon Conservation Centre in California, which engages in bobbing movements of the upper body, while socializing with her male partner. This type of display is likely not idiosyncratic, since it has also been observed in other adult females at the Gibbon Conservation Centre (G. Skollar, pers. comm.), which is one of the few places where captive hoolock gibbons are housed. Further and more systematic observations are needed to sufficiently characterise the occurrence of this behaviour in hoolocks.

Given the behavioural context and structure of the displays described here, it may be tentatively assumed that “jerking body movements” of some form represent homologous social signals in the small ape genera *Nomascus*, *Sympalangus*, and potentially *Hoolock*. Interestingly, gibbon phylogenies based on genomic datasets suggest a derived clade formed by these three genera, with *Hylobates* branching off earlier (Carbone et al. 2014; Shi and Yang 2018). However, given the notoriously conflicting evidence on the topology of the hylobatid family tree (Roos 2016), future studies need to consolidate this phylogenetic hypothesis. In any case, rhythmic presenting might be an interesting model behaviour to study the evolution of gestural signals in small apes. To allow for meaningful comparisons, detailed characterisations of the structure and occurrence of proceptive displays in siamangs and especially hoolocks are needed.

An important question with regards to dance behaviour in gibbons is whether it could be in any way connected to the origins of dance and dance-like gestures in humans. In light of the current evidence, we see no compelling evidence that would merit such a line of inquiry. First, the phylogenetic distance between humans and hylobatids in combination with the scarcity or absence of reports on dance behaviour in the non-human great apes and basal-branched gibbons of the genus *Hylobates* argues against a phylogenetic continuity. Second, the overall structure and occurrence of gibbon dances suggests them to be importantly determined by innate factors, different from human ones. Dance patterns appear to be conserved and uniform between species and are tied to female sexual maturity. Instead, we suggest that human and hylobatid dance, although perhaps based on shared perceptive and sensorimotor principles (see below), originated independently from one another.

4.3 FUTURE PERSPECTIVES

This research and the small number of other available studies on dances in crested gibbons are an initial starting point when it comes to elucidating this behaviour. Next steps should address the investigations of the variability of dances at the individual as well as species level, and studies testing for biological correlates of their structure and frequency. This includes the question of whether the different dance sequences described herein are used to communicate distinct semantic information. Fan et al. (2016) suggested that dances could be a sexually selected behaviour. If so, we would expect that certain aspects of a dance reflect a female's reproductive fitness. In this context, it is important to address why some females dance, while a substantial percentage appear not to, and what causes individuals to stop dancing at some point in their lives. For instance, de Vries (2004) documented a high frequency of dances (70 instances in 28h of observation) in the female Kanak at Apenheul Primate Park in Apeldoorn (*N. leucogenys*; born 1993; ZIMS GAN: MIG12-29829865), which has not been observed to dance in the last 15 years according to our survey response from the corresponding institution.

Other relevant questions concern the structural analysis of dance movements in humans (see, in particular, Charnavel 2019) which has focused on perception, specifically, the idea that humans' perception of dance is shaped by gestalt principles (Wertheimer 1938, and subsequent work). The underlying intuition is that human perception organises a dance sequence into *groups* based on similarity of the movements within a group; significant changes in the movement patterns (such as a change of bodily orientation) will then give rise to the perception of group boundaries (labelled GPRs by Charnavel (2019), following Lerdahl & Jackendoff's (1983) work on music). As of now, we have a very limited understanding of gibbon cognition (see, e.g., King 2021 for recent discussion), which leaves

it unclear whether gibbons exhibit gestalt perception (see, e.g., Hopkins and Washburn (2002) on gestalt perception in chimpanzees vs. its absence in rhesus monkeys). While it is clear that gibbons' dances do not display a similar level of syntactic complexity to what is found in human language, or even in human dance, we demonstrate structural organisation within gibbons' dance sequences that very much resembles the structural organisation of dance movements in humans. Building on the insights from gestalt psychology and dance cognition, important questions going forward concern the level of complexity that can be found in longer dance sequences produced by gibbons, and whether gibbons exhibit similar patterns of gestalt perception as the ones found in humans.

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Credit Statement

Conceptualisation: PPG ; Biological methodology: KRC, CC ; Linguistic methodology: PPG, CC ; Data coding: CC, PPG ; Formal analysis: PPG, CC ; Survey: KRC ; Resources: KRC, PPG ; Data Curation: KRC ; Figures: KRC, PPG, CC ; Writing – Original Draft: CC, KRC ; Writing – Review & Editing: CC, KRC, PPG ; Funding: CC, PP.

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