Full title: Variable expression of linguistic laws in ape gesture: a case study from chimpanzee sexual solicitation.

Short title: Linguistic laws in chimpanzee solicitation gestures.

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Keywords: compression, communication, Zipf, Menzerath, language

Abstract

Two language laws have recently been identified as consistent patterns shaping animal behaviour, both acting on the organisational level of vocal and behavioural communicative systems. Zipf's law of brevity describes a negative relationship between behavioural length and frequency of behaviour. Menzerath's law defines a negative correlation between the number of behaviours in a sequence and the average length of the behaviour composing it. Both laws have been linked with the information-theoretic principle of compression, which tends to minimise code length. We investigate their presence in a case study of male chimpanzee sexual solicitation gesture. While we fail to find evidence supporting Zipf's law of brevity, chimpanzee sexual solicitation gestures follow Menzerath's law, with longer sequences of gestures having shorter average gesture duration. Our results extend previous findings suggesting gesturing can be shaped by individual energetic constraints; however, chimpanzee gesture does not appear to manifest a consistent principle of compression or pressure for efficiency described for most other close-range communication. Importantly, the same signallers and signal set adhered to these laws in subsets of the repertoire when used in play; highlighting that the expression of ape gestures appears shaped by factors such as the immediate socio-ecological context of the interaction.

Introduction

Over the past 100 years, important statistical regularities have been described across human languages and in other communicative systems such as genomes, proteins, and animal vocal and gestural communication (Altmann & Gerlach, 2016; Bentz & Ferrer-I-Cancho, 2016; Börstell et al., 2016; Hernández-Fernández et al., 2019; Köhler et al., 2005; Menzerath, 1954; Naranan & Balasubrahmanyan, 2000; Sanada, 2008; Semple et al., 2022; Wang & Chen, 2015; Zipf, 1936). These regularities are hypothesized to be manifestations of the information theoretic principle of compression (Ferrer-i-Cancho, Bentz, et al., 2022; Semple et al., 2022). Compression is a particular case of the principle of least effort (Zipf, 1949) – a principle that promotes the outcome that requires the least amount of energy to produce or achieve – and thereby promotes coding efficiency (Ferrer-i-Cancho et al., 2013). In communication, compression is expressed as a pressure towards reducing the energy needed to compose a code but limited by the need to retain the critical information in the transmission (Cover & Thomas, 2006; Ferrer-i-Cancho et al., 2020).

Among the statistical patterns predicted by compression at different levels of organization, Zipf's law of brevity and Menzerath's law have been at the centre of recent attention in studies of human and non-human communication. Zipf's law of brevity is the tendency for more frequent words to be shorter in length (Strauss et al., 2007; Zipf, 1949), and is generalised as the tendency for more frequent elements of many kinds (*e.g.*, syllables, words, calls) to be shorter or smaller (Ferrer-i-Cancho et al., 2013) – with similar patterns found at different levels of analysis, for example in speech at the level of words (Strauss et al., 2007) and syllables (Rujević et al., 2021), although not in phonemes (Martindale et al., 2008). As well as being found in human spoken, signed, and written languages (Bentz & Ferrer-I-Cancho, 2016; Börstell et al., 2016; Hernández-Fernández et al.,

2019; Sanada, 2008; Wang & Chen, 2015), Zipf's law of brevity has been identified in the short-range communication of diverse taxa: dolphins (Ferrer-i-Cancho et al., 2022), bats (Luo et al., 2013), penguins (Favaro et al., 2020), hyraxes (Demartsev et al., 2019), and various primates (macaques: Semple et al., 2013; marmosets: Ferrer-i-Cancho & Hernández-Fernández, 2013; gibbons: Huang et al., 2020; Indri indri: Valente et al., 2021), as well as in genomes (Naranan & Balasubrahmanyan, 2000).

At the level of constructs, Menzerath's law states that "*the greater the whole, the smaller its constituents*" (Altmann, 1980; Köhler, 2012; Menzerath, 1954); for example: longer sentences have words of shorter average length, and words with more syllables contain syllables of shorter length. Menzerath's law (and its mathematical expression known as the Menzerath-Altman's law) has been identified in human spoken and signed languages (Altmann, 1980; Andres et al., 2021), genomes (Ferrer-i-Cancho & Forns, 2009; Li, 2012), music (Boroda & Altmann, 1991), and in the communication of dolphins (Ferrer-i-Cancho et al., 2022), penguins (Favaro et al., 2020), and primates (geladas: Gustison et al., 2016; chimpanzees: Fedurek et al., 2017; Heesen et al., 2019; gibbons: Clink et al., 2020; Huang et al., 2020; gorillas: Watson et al., 2020; Indri indri: Valente et al., 2021;). While many studies focused on vocal communication, several have now explored these statistical regularities in gestural and signed domains. For example, the use of Swedish Sign Language in (semi)spontaneous conversation was found to follow a pattern of more frequently used signs being shorter in duration (Börstell et al., 2016). Zipf's law of brevity was also found in fingerspelling, with a negative relationship between mean fingerspelled sign duration and frequency (Börstell et al., 2016). Similarly, Czech sign language was found to follow Menzerath's law (Andres et al., 2021). Work in non-human gesture has, to date, been more focused on context-specific signal usage, for example: Zipf's law of brevity was found in the

surface behaviour of dolphins (such as tail-slapping; Ferrer-i-Cancho & Lusseau, 2009) but not in the play gestures of chimpanzees, although these did follow Menzerath's law (Heesen et al., 2019).

Chimpanzee gestural communication represents a powerful non-human model in which to explore compression and language laws. Apes have large repertoires of over 70 distinct gesture types (Byrne et al., 2017); as compared to vocal communication, gestural repertoires are larger and are more flexibly deployed, with individual gesture types used to achieve multiple goals (Bard et al., 2019; Call & Tomasello, 2007; Hobaiter & Byrne, 2011a; Liebal et al., 2004). Gestures are also used intentionally, *i.e.*, to reach social goals by influencing the receivers' behaviour or understanding (Graham et al., 2018; Hobaiter & Byrne, 2011a, 2014; Schel et al., 2013), and flexibly across contexts (Call & Tomasello, 2007; Hobaiter & Byrne, 2011a; Liebal et al., 2004). Nevertheless, Heesen et al. (2019) only found a pattern coherent with Zipf's law of brevity in subsets of the gestural repertoire, supporting an increasingly diverse range of findings that show variation in the extent and expression of language laws, suggesting that while they appear statistically universal there is room for exceptions and/or variation in patterning at different levels of the communicative construct (Semple et al., 2022).

Although a lack of evidence supporting Zipf's law of brevity has been previously reported (e.g., European heraldry: Miton & Morin, 2019; computer-based neural-networks: Chaabouni et al., 2019), these remain rare exceptions, and in non-human animal communication have typically only been reported in long-distance vocal communication (*e.g.* gibbon song: Clink et al., 2020; bats: Luo et al., 2013; although *cf*. female hyrax calls: Demartsev et al., 2019) where the impact of distance on signal transmission fidelity may

have a particularly strong effect on the costs of compression (Ferrer-i-Cancho et al., 2013; Gustison et al., 2016; Semple et al., 2022). Thus, at present, the repertoire-level absence of Zipf's law of brevity in chimpanzee gesture remains a conundrum.

One explanation – like the case for long-distance signals – is that the context in which it is produced may have impacted its expression. In this case, the use of gestures from within play. Expressions of linguistic laws in biological systems reflect pressures that shape efficient energy expenditure (Semple et al., 2022). Play is produced when there is an excess of time and energy (Held & Špinka, 2011; Pellis & Pellis, 1996; Smith, 2014), thus, the energetic need to reduce signal effort through increased compression may be limited. As a result, it remains unclear whether the failure of Zipf's law of brevity in chimpanzee gesture was due to the use of gestures from within play, or whether it reflects a system-wide characteristic.

Another possible explanation is that the ability to detect linguistics laws, particularly where they are only subtly expressed, may require powerful datasets. The exploration of statistical patterns in human languages often employs corpora containing millions of data points (e.g., Hatzigeorgiu et al., 2001). In contrast, in ape gesture, as in many studies of non-human communication, datasets are substantially smaller (in the thousands). In chimpanzee play, the large repertoire expressed limits the frequency with which particular gesture types are represented.

We address this open question in a case study of chimpanzee gestural communication in sexual solicitation. While gesture is relatively under-studied in this area, sexual solicitations have been contrasted with early descriptions of gesture from studies of

136 captive ape play, as an example of gesture in a relatively more 'urgent' context for
137 communication (Hobaiter & Byrne, 2012; *c.f.* Call & Tomasello, 2007). Chimpanzees,
138 particularly male chimpanzees, employ prolific use of individual gestures and gesture
139 sequences in sexual solicitations. Often vigorous, solcitations incorporate regular use of
140 gesture types that include both visual and audible information (Hobaiter & Byrne, 2012;
141 Nishida, 1980). While a range of gesture types are employed, these are typically a smaller
142 sub-set of the available repertoire – as opposed to play where the majority of gesture types
143 are deployed. Successful gestures can lead directly to sexual behaviour, such as inspection
144 or copulation, as well as to a consortship, in which the female follows the male away from
145 other individuals in the group so that he maintains exclusive sexual access (Tutin, 1979).
146 Both direct solicitation and consortship and are key strategies for individual fitness (Tutin,
147 1979; Watts, 2015), and as such behaviour associated with them is likely subject to strong
148 selective pressures. The energetic costs of lactation mean that adult female chimpanzees
149 typically concieve only once every 4-5years (Clark, 1977; Thompson, 2013). So while there
150 are typically 60-80 individuals in a group, the operational sex ratio of available females in
151 estrus may be very small, and males show substantial variation in reproductive success
152 (Newton-Fisher et al., 2009; Tutin, 1979). Although highly important, the performance of
153 sexual solicitations may come with significant costs: besides the energetic expenditure in
154 producing these signals, there is a risk of potentially aggressive competition both from other
155 males in their own community (Fawcett & Muhumuza, 2000; Tutin, 1979) as well as
156 potentially lethal competition from males in neighbouring groups (Wilson et al., 2014). Thus,
157 there are substantial advantages to avoiding potential eavesdroppers within, and
158 particularly outside of, one's community (Hobaiter et al., 2017). Therefore, on one hand
159 individuals benefit from producing conspicuous energetic signals to attract females, often

160 having to insist to secure mating; on the other, the production of highly conspicuous signals
161 should be compressed to reduce the risks associated with competition from both within and
162 outside the group.
163
164 We test for patterns predicted by Zipf's law of brevity and Menzerath's law, both at
165 the level of single gesture types and gesture sequences, respectively. To investigate Zipf's
166 law of brevity and Menzerath's law we fit two generalised linear mixed models. The first
167 model will explore the presence of Zipf's law assigning gesture duration as the response
168 variable, proportion of gestures within the dataset and category of gesture (manual vs
169 whole body) as fixed factors, and signaller's ID, sequence ID, and gesture type as random
170 factors. The second model will test for Menzerath's law and will have gesture duration as
171 response variable, sequence size as a fixed factor, and proportion of whole-body gestures in
172 the sequence (PWB), signaller ID, sequence ID, and gesture type as random factors. We
173 included information on the category of the gesture to allow for comparisons with human
174 studies, in which gestures are mostly manual. We provide paired models that describe the
175 patterns of expression both across all males in our data and for a single prolific individual. In
176 doing so, we provide an initial assessment of the likely generalizability of our findings across
177 male chimpanzee gesturing in this context, and provide a robust novel assessment of
178 compression in ape gestural communication**.**
179

180 **Results**

181 We measured *N*=560 sexual solicitation gestures from 173 videos of 16 wild, habituated
182 male East African chimpanzees (*Pan troglodytes schweinfurthii*) gesturing to 26 females.

Within the 560 gestural instances (from now *tokens*), we identified 26 gesture types: 21 manual gestures and 5 whole-body gestures (Figure 1; for definitions for full repertoire definitions see Table S8 in Supporting Information S4) performed by 16 male chimpanzees aged 10-42 years old. On average, each individual produced a median of 11.5 ± 70.7 gesture tokens (range 2-290). One male, Duane, was particularly prolific (n=290 gesture tokens; other males 2-76). To provide context as to what extent our findings are generalizable, we provide matched analyses using both the full dataset and the dataset limited to Duane only.

Gesture token duration was measured via analysis of video data with a minimum unit of 0.04s (one frame). Duration ranged from 0.04-15.04 seconds (median: 1.56 ±2.35s). If consecutive gesture tokens were performed with less than 1s in between them, they were considered to form a sequence (Heesen et al., 2019; Hobaiter & Byrne, 2011b). We detected a total of 377 sequences, with each male performing a median of 8 ±44.54 sequences (range 1-181 sequences). Sequence length ranged from 1 to 6 tokens (Table 1). For analyses of Menzerath's law we excluded 18 sequences for which we were unable to identify the duration of all the consecutive gesture tokens performed, resulting in the analysis of 359 sequences, containing a total of 530 gesture tokens. 244 sequences were composed of a single token, the remaining 115 sequences had length n>1. Of the 115 sequences analysed that were composed of 2 or more gesture tokens; 26 (23%) were formed by the repetition of the same gesture type, whereas the remaining 89 (77%) included more than one gesture type (Table 1).

Do chimpanzee sexual solicitation gestures follow Zipf's law of brevity?

To test for Zipf's law we ran a Bayesian generalised linear model (Zipf-model), with the log of gesture duration as the response variable and the proportion of gesture type within the dataset as a fixed factor (see Supporting information 2 for further detail). We included category of gesture as a control, and signaller ID, sequence ID, and gesture type as random factors. The Zipf-model fit the data better than a null model that did not include the proportion of gesture type as a fixed effect (Leave-one-out [LOO] difference = -0.7 ± 0.3). For Zipf-model effects Bulk ESS and Tail ESS were >100 and Rˆ<1.01. However, the proportion of gesture type did not have a substantial effect on the duration of gestures (Supporting information 3, table S4; b = 0.90, s.d. = 1.26, 95% CrI [−1.25, 3.81]). When testing the subset of data containing only the gestures produced by Duane, the full model and null model testing for Zipf's law showed similar fit (LOO difference: -0.3 ± 0.5; Supporting information S3, Table S5).

Do chimpanzee sexual solicitation gesture sequences follow Menzerath's law?

To test for Menzerath's law we ran a second Bayesian model (Menzerath-model) with the log of the gesture duration as response variable, the sequence size as fixed factor, the proportion of whole-body gestures within the sequence (PWB) as a control, and the signaller ID and sequence ID as random factors. The Menzerath-model fit the data better than the null model (LOO difference: -7.9 ± 4.0). All predictors had Bulk ESS and Tail ESS>100 as well as R^ values <1.02. Sequence size had a significant negative effect on gesture duration within sequence (Supporting information 3, Table S6; b = -0.18, s.d. = 0.04, 95% CrI [0.26, -0.11]; Figure 2). Similar results were found when running the same Menzerath-model but limited to gestures produced by Duane: the full model fitted the data better than the

null (LOO difference: -14.0 ± 4.4), all predictors had Bulk ESS and Tail ESS>100, R^<1.01 and sequence size had a significant negative effect on gesture duration (Supporting information 3, Table S7, Figure 3; b = -0.25, s.d. = 0.04, 95% CrI [-0.33, -0.16];). We note that the sample size of sequences of four tokens or longer is smaller than those of one to three tokens (Table 1), which may have contributed to the apparent tailing off of a clear relationship in Figure 2 and Figure 3.

Discussion

Chimpanzee sexual solicitation gestures did not follow Zipf's law of brevity: the frequency of gesture type within the dataset did not predict gesture duration. However, sequences of chimpanzee solicitation gestures did follow Menzerath's law: longer sequences of gestures were made up of gestures of shorter average length. Our dataset was limited both by its relatively small size (*c.f.* Heesen et al., 2019 on chimpanzee play gestures) and in its bias towards a single highly prolific individual. As a result we consider it a case-study; nevertheless, our findings were similar for both the full dataset across male signallers, and for a single prolific individual, as well as in a range of alternative analyses (Supporting Information 1), suggesting that the pattern of results appears to be relatively robust.

These results represent a further absence of evidence in support of Zipf's law of brevity in great ape gestural communication (Heesen et al., 2019) and support the wider finding that – unlike most other close-range systems of communication described to date – the expression of pressure for compression and efficiency may be variably expressed in ape gesture (Börstell et al., 2016; Ferrer-i-Cancho et al., 2013; Semple et al., 2022). It particularly highlights that compression does not act on communicative systems uniformly: 20 of the 26 gesture types described here as used in sexual solicitations overlapped with those used in play (Heesen et al., 2019). Data were collected from the same community over the same period, and although both studies provided a null result when analysing the full gestural repertoire, Zipf's law was found in subsets of the play gestures but not in the gestures when used in sexual solicitations. Moreover, when running traditional correlation analyses in which features such as signaller identity, or gesture type could not be controlled for, we found a tendency for an opposite Zipf's law pattern – particularly in manual gestures (Supporting Information 1). Visual inspection of the Figures 2 and 3 shows the substantial

variation in the duration of gestures across instances of communication, as well as an apparent decrease in a clear relationship between gesture duration and sequence size where sample size was small (such as for longer sequences). Together these findings suggest that the expression of these laws is nuanced by aspects of the communicative landscape in which they are deployed, and that large samples may be needed to detect sometimes subtle relationships. As Semple et al. (2022) suggest, apparent 'failures' may be of substantial assistance in exploring the boundaries of the theoretical framework of these laws, helping to define the characteristics that shape both their emergence and variation in their expression.

In contrast to vocal communication across primate species, in chimpanzee sexual solicitations 'inefficiency' in signalling effort by the signaller appears to be at times slightly favoured. However, these gestures appear to remain effective in terms of achieving the signaller's goal of successful communication in a context vital for reproductive success. Given the long inter-birth intervals and active mate guarding (Muller & Wrangham, 2009), chimpanzee paternity is often heavily biased towards higher-ranking individuals (Newton-Fisher et al., 2009). With so few opportunities to mate, sexual solicitations may represent one of the most evolutionarily important contexts in which chimpanzee gestures are produced. Where the costs of signal failure are high, there is a pressure against compression and towards redundancy, as in chimpanzees' use of gesture-vocal signal combinations in agonistic social interactions (Hobaiter et al., 2017). While there are examples of vocal communication systems used in urgent contexts that adhere to Zipf's brevity law (Favaro et al., 2020), the benefits of successful communication to individual fitness in chimpanzee solicitation appear to outweigh the energetic costs associated with the production of a

vigorous and conspicuous signal. Nevertheless, given that we see a relatively consistent expression of Menzerath's law across gesture use in sexual solicitation as in play, even the production these prolonged and conspicuous signals appear to remain constrained by physiological mechanisms of gestural production. As for primate vocal communication (Fedurek et al., 2017; Gustison et al., 2016), where breathing constraints and energetic demands of vocal production were considered drivers for the emergence of Menzerath's law patterns, increased muscular activity related to the production of sequences of gestures (Scott, 2008) could be a general limit on energetic investment. As a result, Menzerath's law appears to emerge across communicative contexts.

There are a number of potential reasons for why language laws appear variable in their expression within ape gesture. One factor may be what is currently being measured. In human speech, sign, and gesture – as in other communication systems – it is possible to consider the production of a 'unit' of communication at different levels. For example, while Zipf's law is clearly expressed in the words and syllables of spoken languages (Rujević et al., 2021; Strauss et al., 2007), that is not the case in phonemes (Martindale et al., 2008). Conversely, in Börstell et al. (2016) research on Swedish Sign Language, Zipf's law of brevity seems to hold across sign categorisation, fingerspelling, and compounding. Interestingly, this study excluded the hold phase of a sign, limiting their analysis only to the more active stroke phase. In both signed languages and human gesturing, distinctions are made between different components of their production. For example: preparative movements, the action stroke that distinguishes the sign itself, a hold or repetition of the action, and the recovery as the hands return to rest (Kendon, 2004). For example: in a reach gesture this would correspond to the movement of the hand into position, the extension of the arm and

hand towards the recipient, the maintenance of the extension, and the return of the hand and arm to a resting state. All four of these phases require some energetic investment to produce, but there may be variation across them. Aspects such as preparation and recovery may be nearly or entirely absent where several gestures are strung together. The production of intentional gestures in apes are shaped not only by the signaller, but by the interaction between signaller and recipient (Byrne et al., 2017; Graham et al., 2022). As a result, the duration of hold or repetition phase may be shaped by the immediate context of the specific interaction – for example, in waiting for a response by the recipient it may vary between being absent and very prolonged. In contrast, the action stroke of a sign or gesture is always present, and represents the need to convey information in that gesture, i.e., to discriminate it from other gesture actions. In Swedish Sign Language a prolonged and repetitive feedback sign and prolonged turn taking signs were the only two cases that diverged from the general Zipf's pattern, as they were both long in duration as well as being highly frequent (Börstell et al., 2016). Zipf's law acts on a signal 'type' in an individual's or species' repertoire – and it may be of interest to compare its expression across areas of gesture production that are more consistently produced across usage, such as the action stroke.

Research to date has typically focused on signal compression at the level of the communication system, but communication happens *in-situ*. Signallers likely respond to pressures on signalling efficiency more broadly: an intense but time-limited investment in clear signalling may be more energetically efficient than the need to travel with a female for extended periods following a failed signal. A similar solicitation with a different audience may need to be produced rapidly and inconspicuously, as the detection of this activity by other males could be fatal (Fawcett & Muhumuza, 2000). In a recent human study,

329 pressures towards efficiency and accuracy were both required for Zipf's law of brevity to
330 emerge in experimental communicative tasks between two participants (Kanwal et al.,
331 2017). Conversely, when participants were required to produce solely time-efficient vs
332 solely accurate communicative signals no pattern emerged. The sexual solicitation context
333 tested in our study may mirror the pattern seen in the time-efficient paradigm in the human
334 study. In play, where urgency and time-efficiency may be less relevant, the same signals
335 used by the same chimpanzees did show compression. While many vocalizations are
336 relatively fixed, gestural flexibility (in goal and context – Bard et al., 2019; Call & Tomasello,
337 2007; Hobaiter & Byrne, 2011a; Liebal et al., 2004) allows us to explore how compression
338 acts within both specific instances of communication as well as on whole communication
339 systems. To do so will require large longitudinal datasets in which it is possible to test both
340 individual variation and variation within individuals across different gesture types and
341 sequence lengths. Similarly, there remains substantial work needed to explore variation
342 across different socio-ecological contexts of gesture use, for example in the social
343 relationship between the signaller and recipient (Graham et al., 2022). The use of
344 redundancy within specific subsets of gesture, or within specific contexts of gesture
345 demonstrates both the importance of compression in communicative systems in general,
346 but also the flexibility present in each specific usage. In doing so, it highlights the
347 importance of exploring the impact of individual and socio-ecological factors within wider
348 patterns of compression in biological systems in evolutionary salient scenarios.
349

350 **Methods**

We measured *N*=560 male to female sexual solicitation gestures from 173 videos recorded within a long-term study of chimpanzee gestural communication depicting 16 wild, habituated East African chimpanzees (*Pan troglodytes schweinfurthii*) from the Sonso community of the Budongo Forest Reserve in Uganda (1°35' and 1° 55'N and 31° 08' and 31°42' E), collected between December 2007 and February 2014. Observations were made between 7.30am and 4.30pm with recording of gestures following a focal behaviour sampling approach (Altmann, 1974). Here, all social interactions were judged to have the potential for gesture, in practice any situation in which two chimpanzees were in proximity and not involved in solitary activities, were targeted. Where several potential opportunities to record co-occurred, preference was given to individuals from whom fewer data had been collected (with a running record of data collection maintained to facilitate these decisions).

During October 2007 to August 2009 a Sony Handycam (DCR-HC-55) was used. Here video was recorded on MiniDV tape. The challenges of filming wild chimpanzees in a visually dense rainforest environment meant that, at times, the start of gestural sequences was not captured on video. Where this occurred, it was dictated onto the end of the video and these sequences were not included in analysis. Similarly, sequences in which part of the sequence was obscured, for example where a chimpanzee moves through dense undergrowth, were also discarded. After 2009 video data were collected using Panasonic camcorders (V770, HC-VXF1) were used which have a 3-second pre-record feature that improves the ability to capture the onset of behaviour; however, the same procedure was used and any sequences where the onset of gesturing was not clearly captured continued to be discarded.

Sexual solicitation gestures

Sexual solicitation gestures were defined as those gestures given by a male towards a female with the goal of achieving sex, usually accompanied by the male having an erection and the female being in oestrus (Hobaiter & Byrne, 2011a, 2012). We included solicitations in the context of sexual consortship; here a male gestures in order to escort a female away from the group to maintain exclusive sexual access, which can occur prior to the peak of the female oestrus (Tutin, 1979). We restricted our analyses to male to female sexual solicitation, as female to male sexual solicitation attempts rarely involved sequences of gestures in this population. We further restricted analysis to solicitations by male individuals of at least 8-years old, as this is the minimum age of siring recorded in this community, limiting our signals to those on which there is more direct selective pressure.

Defining gesture types and tokens

In quantitative linguistics, word *types* are used to assess Zipf's law of brevity, whereas *tokens* are used to assess patterns conforming to Menzerath's law. To distinguish the two, consider the question:

Which witch was which?

The question is composed of 4 *tokens* (overall word count), and three different word *types*, (which, witch, was). Gesture *types* (see S4 Table for a detailed repertoire description) were categorized according to the similarity of the gesture movement, which could be used either as a single instance or in a sequence; and each gestural instance represented an individual *token*.

Great apes deploy gestural sequences in two distinct forms (Hobaiter & Byrne, 2011b): one is the addition of further gestures following response waiting and is typically described as persistence (which may include elaboration). The second is the production of gestures in a

‘rapid sequence’ – here gestures are produced with less than 1 second between consecutive gesture tokens, and do not meet behavioural criteria for response-waiting occurring within a sequence (although it may occur at the end of it). As the expression of Menzerath’s law is typically considered at the level of a unique sequence, rather than one generated through the addition of gestures in response to earlier failure, we limit our analyses here to rapid sequences only. Sequence length was quantified as the number of gesture tokens produced with less than 1s between two consecutive gesture tokens; single gestures were coded as sequences of length one (Heesen et al., 2019; Hobaiter & Byrne, 2011b).

Gesture duration

Gesture duration was calculated using MPEG streamclip (version 1.9.3beta). We measured gesture duration in frames, each lasting 0.04s. Gestural ‘units’ – like many other signals – can be considered at different levels of analysis, for example: a word is composed of syllables, and syllables of phonemes. Gestures have been described as composed of a preparation, action stroke, hold or repetition, and recovery phase (Kendon, 2004). Here we follow previous work in (Heesen et al., 2019) in defining the start of a gesture token as the initial movement of a part of the body required to produce the gesture. The end of a gesture token corresponded to (1) the cessation of the body movement related to gesture production, or (2) a change in body positioning if the gesture relied on body alignment, or (3) the point at which the goal was fulfilled, and any further movement represented effective action (for example, locomotion or copulation). Where the expression of a gesture token did not include a full recovery (in which the body part involved is returned to a resting state), the end of a token was discriminated from subsequent tokens through (1) a change in gesture action, e.g., from a reach to a shake, (2) a change in the rhythm or orientation of

420 a gesture action, hold, or repetition, e.g., the rhythm or direction of an object shake is
421 broken or changed (Hobaiter & Byrne, 2017).
422
423 **Intra-observer reliability**
424 Intra-observer reliability was tested by randomizing the order of the videos and re-coding
425 the duration of the gestures of every ninth clip, for a total of 75 gestures from 23 clips. We
426 performed an intraclass correlation coefficient (ICC) test – class 3 with *n*=1 rater (Landers,
427 2015) – which revealed very high agreement on gesture duration measurements (ICC=0.995,
428 *p*<.001).
429
430 **Statistical analysis**
431 All data were analysed using R version 4.0.0 and RStudio version 1.2.5042 (R Core Team,
432 2020; RStudio Team, 2020).We fitted Bayesian generalised linear multivariate multilevel
433 models using the 'brm' function from the 'brms' package (Bürkner, 2017) with minimally
434 informative priors, 2000 iterations and 3 chains.
435 We ran a first model testing Zipf's law of brevity (Zipf-model), containing gesture
436 token duration (s) as the response variable, the proportion of occurrences of a particular
437 gesture type in the dataset (Proportion) as a fixed effect, and gesture Category (manual vs
438 whole-body) as a control. We included signaller ID, sequence ID, and gesture type as
439 random effects. We include Category as a variable here to allow for more direct comparison
440 with previous work, which often excludes or differentiates non-manual signals, either in
441 great ape gesture (Heesen et al., 2019; Rodrigues et al., 2021) or in signed languages and
442 fingerspelling (e.g., Börstell et al., 2016).

We tested Menzerath's law by running a second model (Menzerath-model) containing gesture token duration (s) as the response variable, sequence size (number of gesture tokens within the sequence) as a fixed factor, and the proportion of whole-body gestures within the sequence (PWB) as a control. We modelled signaller ID and sequence ID as random factors.

As our data may be particularly influenced by a single prolific individual (Duane) who contributed around half of the data, we assess the generalizability of our findings by replicating analyses conducted on the full dataset on a subset of the data containing only gestures by Duane. For the models testing Duane's data, signaller ID was removed from the random factors.

We ran full-null model comparisons using the Level One Out information criterion (LOO) (Vehtari et al., 2017) 'loo_compare' function from the 'stan' package (version 2.21.5; (Stan Development Team, 2022) where Zipf's null model contained only the control variable Category and the random effects, whereas Menzerath's null model contained only the control variable PWB and the random effects. Prior to the Bayesian analysis we assessed data distribution using the 'fitdistr' package (version 1.0-14;(Delignette-Muller & Dutang, 2015). Following data inspection, we log-transformed gesture duration and average sequence duration as data from the response variable strongly skewed towards zero (for data inspection see supporting information 2).

Finally, previous work has frequently employed correlation and compression tests, which looks at whether the expected mean code length observed in the dataset is significantly

smaller than a range of mean code lengths calculated via permutations, to test the mathematical theory behind both laws. These tests offer limited opportunities to control for potential confounds such as signaller identity and should be used with particular caution in relatively small and variable datasets. We provide them in the Supporting Information 1 to allow for comparison with previous work.

Data and code

Data and code for all analyses are available in a public GitHub repository: https://github.com/Wild-Minds/LinguisticLaws_Papers and have been archived within the Zenodo repository https://zenodo.org/record/6802831#.YsWh7-zMI0Q

Acknowledgements

We thank the staff and field assistants of the Budongo Conservation Field Station for their assistance in the original gestural data collection, and the Ugandan National Council for Science and Technology and the Ugandan Wildlife Authority for permission to conduct the original research. We thank the Royal Zoological Society of Scotland for its funding of the field station. We thank Dr Alexander Mielke for his advice on the statistical models. We thank the editor and three anonymous reviewers for their constructive comments. This research received funding from the European Union's 8th Framework Programme, Horizon 2020, under grant agreement no 802719.

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Table 1. Number of sequences composed of the same or different gesture types, listed according to sequence length.

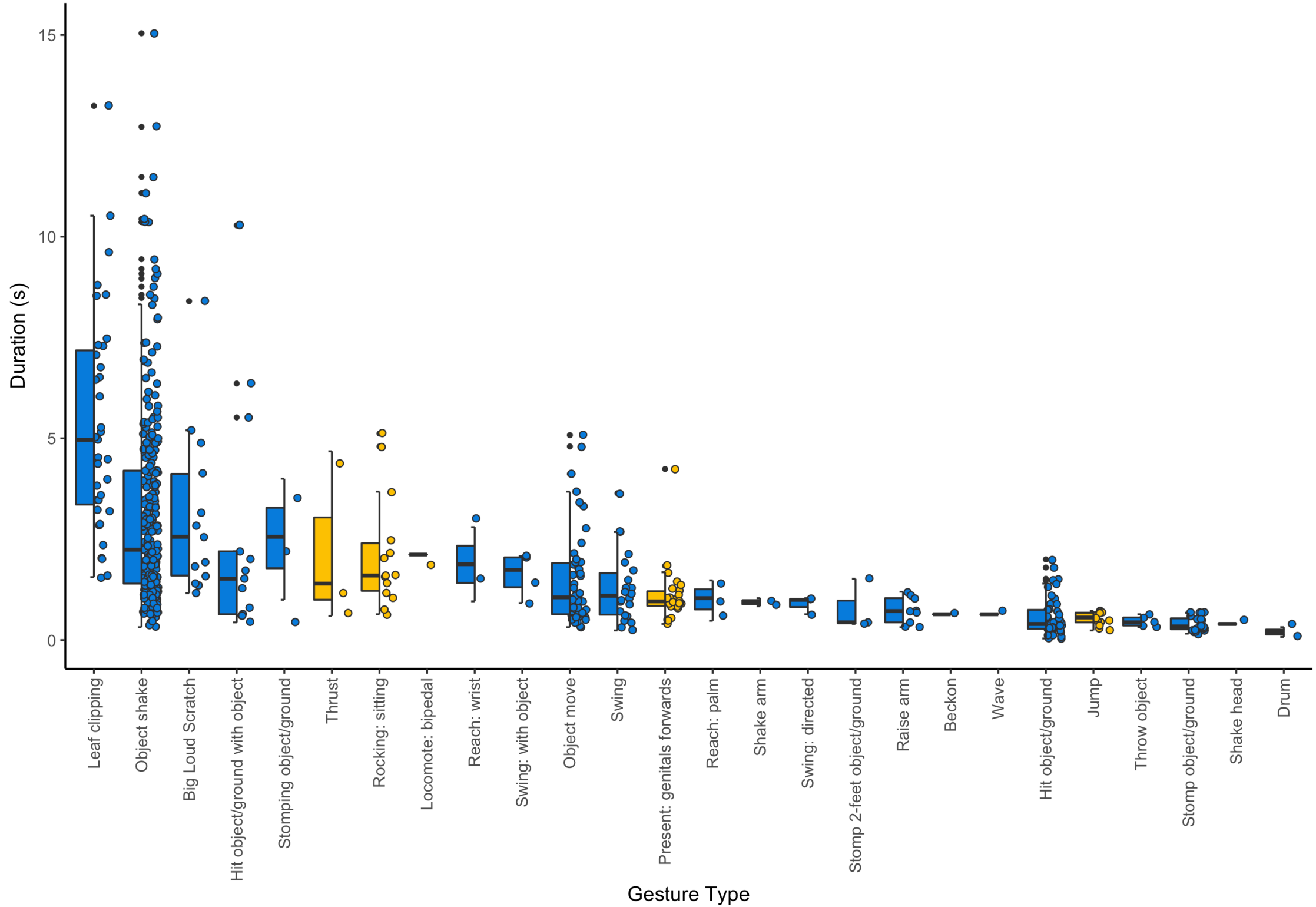
Sequence length is defined by the number of gesture tokens present in the sequence.

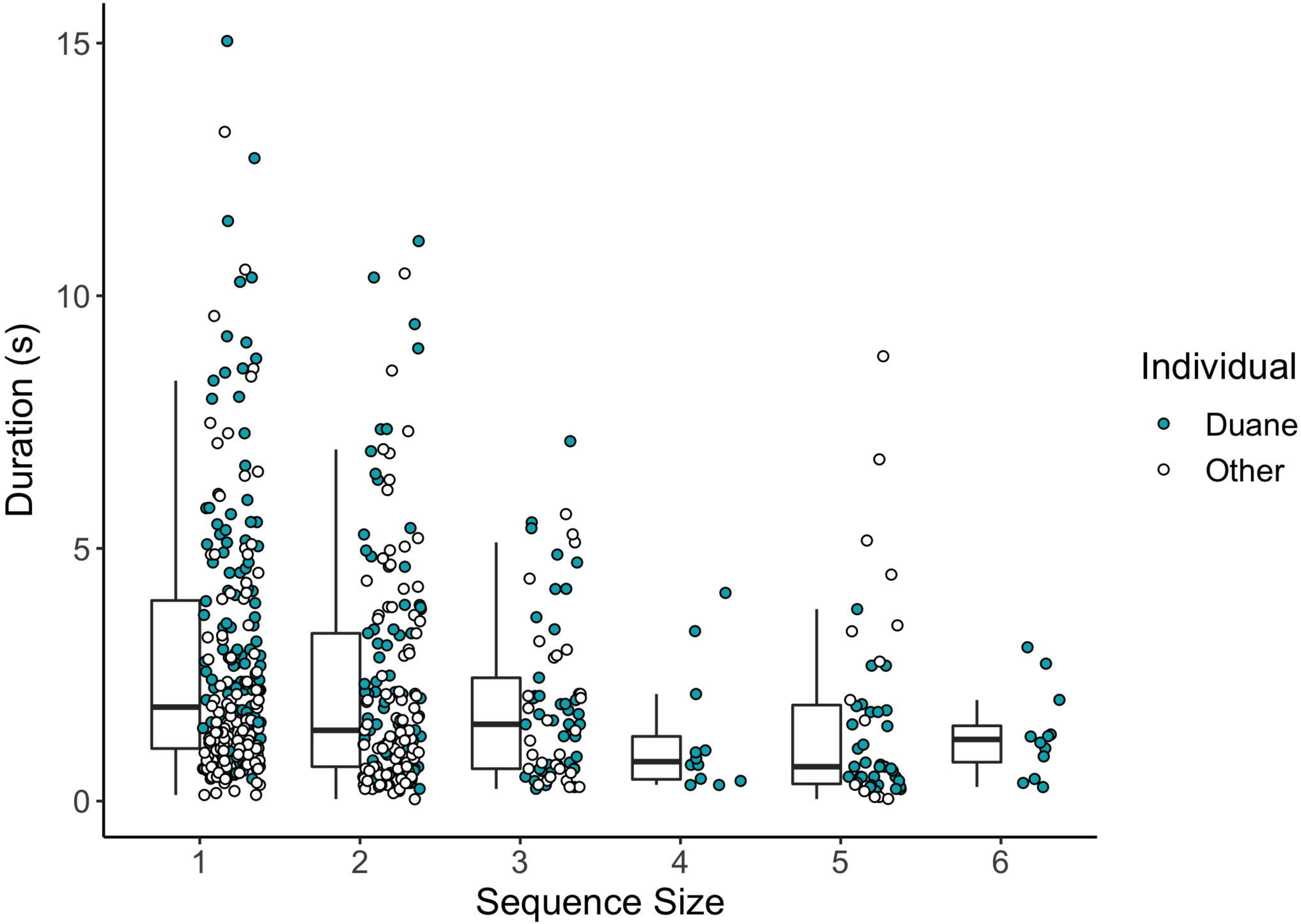
Figure 1. Distribution of gestural instances across the 26 gesture types detected with relative gesture duration. Boxplots represent the median (black bar), the interquartile range – IQR (boxes), maximum and minimum values excluding outliers (whiskers) and outliers (black dots). Points represent individual gestures. Whole-body gestures are indicated in yellow, manual gestures in blue.

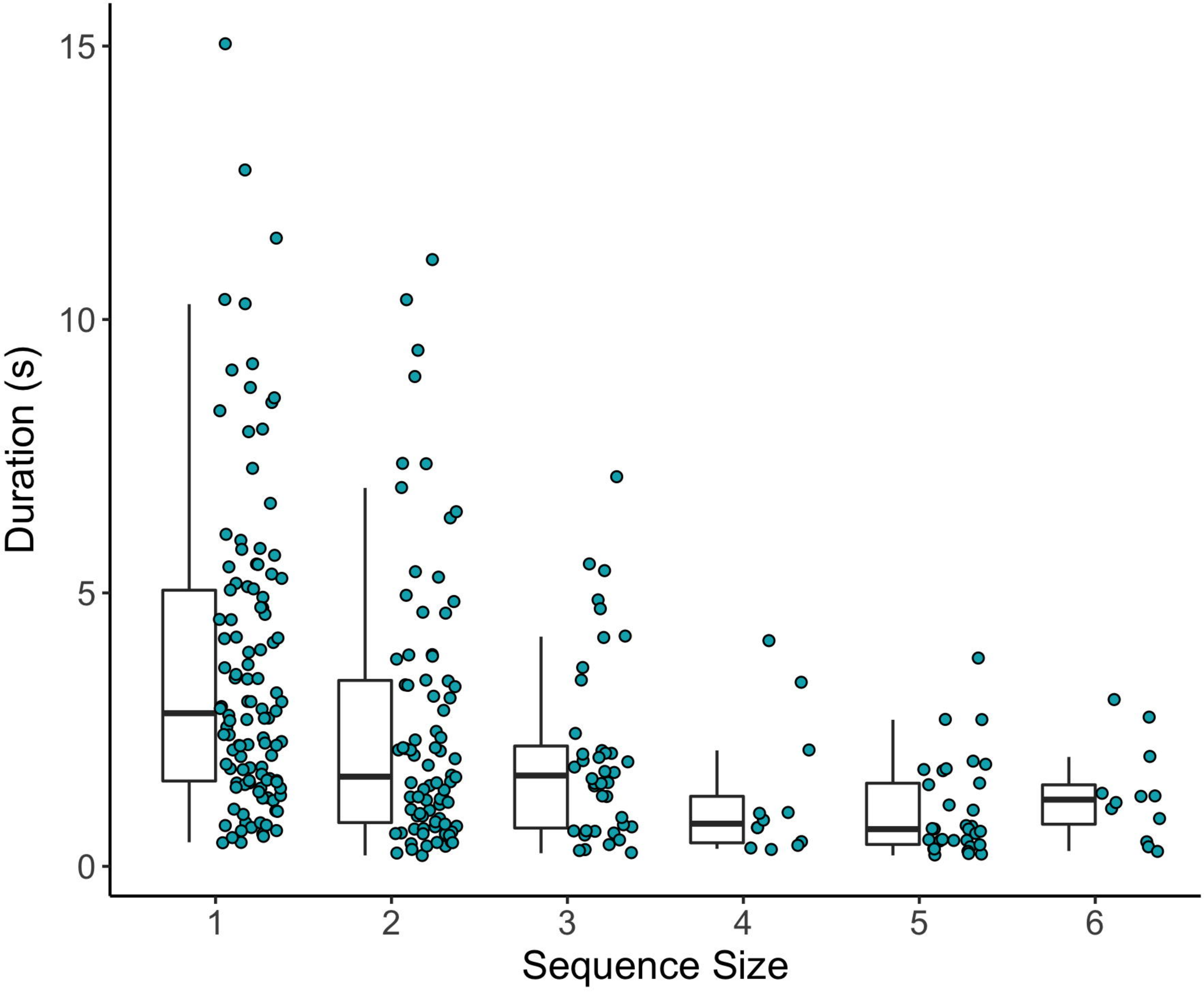
Figure 2. Relationship between sequence size and gesture duration for the full dataset. Boxplots represent the median (black bar), the interquartile range – IQR (boxes), and maximum and minimum values excluding outliers (whiskers). Points represent gesture tokens. Gestural tokens belonging to the individual Duane are indicated in light blue. White circles indicate gesture tokens belonging to all other individuals.

Figure 3. Relationship between sequence size and gesture duration for the dataset containing only gestures performed by *Duane.*

Boxplots represent the median (black bar), the interquartile range – IQR (boxes), and maximum and minimum values excluding outliers (whiskers). Points represent gesture tokens.


Duration (s)
15
10
5
0
Leaf clipping
Object shake
Big Loud Scratch
Hit object/ground with object
Stomping object/ground
Thrust
Rocking: sitting
Locomote: bipedal
Reach: wrist
Swing: with object
Object move
Swing
Present: genitals forwards
Reach: palm
Shake arm
Swing: directed
Stomp 2-feet object/ground
Raise arm
Beckon
Wave
Hit object/ground
Jump
Throw object
Stomp object/ground
Shake head
Drum
Gesture Type


Duration (s)
15
10
5
0
1
2
3
4
5
6
Sequence Size
Individual
Duane
Other


15
10
5
0
Duration (s)
1
2
3
4
5
6
Sequence Size