



This postprint was originally published by the APA as:
Florkiewicz, B. N., Oña, L. S., Oña, L., & Campbell, M. W. (2024).
**Primate socio-ecology shapes the evolution of distinctive facial
repertoires.** *Journal of Comparative Psychology*, 138(1), 32–44.
<https://doi.org/10.1037/com0000350>

Supplementary material to this article is available. For more information see
<https://hdl.handle.net/21.11116/0000-000D-1F5B-C>

The following copyright notice is a publisher requirement:

©American Psychological Association, 2024. This paper is not the copy of record and may not exactly replicate the authoritative document published in the APA journal. Please do not copy or cite without author's permission.

The final article is available, upon publication, at:

<https://doi.org/10.1037/com0000350>

Provided by:

Max Planck Institute for Human Development

Library and Research Information

library@mpib-berlin.mpg.de

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Primate Socio-Ecology Shapes the Evolution of Distinctive Facial Repertoires

BRITTANY N. FLORKIEWICZ^{1*}, LINDA S. OÑA², LEONARDO OÑA³, MATTHEW W.
CAMPBELL⁴

¹ Department of Psychology, Lyon College, Batesville, Arkansas, U.S.A.

*² Max Planck Institute for Human Development, Max Planck Research Group 'Naturalistic
Social Cognition', Berlin, Germany*

³ Department of Ecology, Faculty of Biology, Osnabrück University, Osnabrück, Germany

*⁴ Department of Psychology, California State University Channel Islands, Camarillo, California,
U.S.A.*

*Corresponding Author

Email for correspondence: Brittany.florkiewicz@lyon.edu

17 **Keywords:** facial signals; chimpanzees; gibbons; communication; sociality

18 **ABSTRACT**

19 Primate facial musculature enables a wide variety of movements during bouts of
20 communication, but how these movements contribute to signal construction and repertoire size is
21 unclear. The *facial mobility hypothesis* suggests that morphological constraints shape the
22 evolution of facial repertoires: species with higher facial mobility will produce larger and more
23 complex repertoires. In contrast, the *socio-ecological complexity hypothesis* suggests that social
24 needs shape the evolution of facial repertoires: as social complexity increases, so does
25 communicative repertoire size. We tested these two hypotheses by comparing chimpanzees (*Pan*
26 *troglodytes*) and gibbons (family *Hylobatidae*), two distantly related apes who vary in their facial
27 mobility and social organization. While gibbons have higher facial mobility than chimpanzees,
28 chimpanzees live in more complex social groups than gibbons. We compared the morphology
29 and complexity of facial repertoires for both apes using Facial Action Coding Systems designed
30 for chimpanzees and gibbons. Our comparisons were made at the level of individual muscle
31 movements (AUs) and the level of muscle movement combinations (AU combinations). Our
32 results show that the chimpanzee facial signaling repertoire was larger and more complex than
33 gibbons, consistent with the *socio-ecological complexity hypothesis*. On average, chimpanzees
34 produced AU combinations consisting of more morphologically distinct AUs than gibbons.
35 Moreover, chimpanzees also produced more morphologically distinct AU combinations than
36 gibbons, even when focusing exclusively on AUs present in both apes. Therefore, our results
37 suggest that socio-ecological factors were more important than anatomical ones to the evolution
38 of facial signaling repertoires in chimpanzees and gibbons.

39

40 INTRODUCTION

41 Relative to other animals, primates produce a wide variety of facial muscle movements
42 during bouts of social communication (Darwin, 1872; Van Hooff, 1967). As a result, primates
43 have rich repertoires of stereotyped facial signals that can be used to communicate emotions and
44 intentions (Ekman, 1970; Van Hooff, 1967; Demuru et al., 2015; Waller et al., 2016). Recent
45 studies have found that the ability to produce certain kinds of facial muscle movements are
46 restricted to select primate species (Waller et al., 2020), which could impact the size and
47 complexity of facial signaling repertoires (Dobson, 2009). Additional studies have found that
48 some stereotyped facial signals are produced across a wide variety of primate species (such as
49 the play face; Preuschoft, 2000; Preuschoft & van Hooff, 1997), whereas others appear to be
50 restricted to a smaller number of species (such as the raspberry face; Hopkins et al., 2007). There
51 are two proposed explanations for the presence of variability among primates regarding facial
52 muscle movements and stereotyped facial signals.

53 One explanation is that greater facial mobility (i.e., the number of independent facial
54 muscle movements that a given species has been observed to produce) results in greater
55 communicative complexity within a given species (Dobson, 2009). Primates who exhibit a
56 greater proportion of slow-twitch muscle fibers (which are necessary for fine-grained motor
57 control of the face; Burrows et al., 2014; Burrows et al., 2016) and a discrete number of facial
58 muscle movements (Waller et al., 2020) may produce larger and more complex facial signaling
59 repertoires. We refer to this as the *facial mobility hypothesis*. An alternative explanation is that
60 social complexity (based on the number of individuals and/or social interactions) results in
61 greater communicative complexity within a given species (Freeberg et al., 2012). Primates who
62 live in larger social groups (with numerous individuals) and have frequent social interactions

63 across many different contexts may produce larger and more complex facial signaling repertoires
64 (Freeberg, 2006; Freeberg et al., 2012). We refer to this as the *socio-ecological complexity*
65 *hypothesis*.

66 Our current study aims to test the *facial mobility hypothesis* and the *socio-ecological*
67 *complexity hypothesis* using facial signaling data from gibbons (family Hylobatidae) and
68 chimpanzees (*Pan troglodytes*). While gibbons and chimpanzees are both hominoids, they are
69 separated by at least 20 million years of evolutionary history (Glazko & Nei, 2003). As a result,
70 gibbons and chimpanzees exhibit variations in their facial anatomy and social behavior, which
71 could directly impact the size and complexity of their facial repertoires.

72 *Facial Morphology*

73 Gibbons and chimpanzees differ in both body size (with chimpanzees being larger-bodied
74 than gibbons), coloration, and facial morphology (Campbell et al., 2010). Gibbons have many
75 documented facial muscle movements (N=20; Waller et al., 2012) and can use these movements
76 to produce up to 80 morphologically distinct facial signals (or combinations of facial muscle
77 movements; Scheider et al., 2014; Florkiewicz et al., 2018). In contrast, chimpanzees have five
78 fewer documented facial muscle movements than gibbons (N=15; Vick et al., 2007). Previous
79 studies with chimpanzees have found that these 15 facial muscle movements are associated with
80 the production of 9 prototypical facial signaling categories (Vick et al., 2007). However, no
81 studies to date have reported on the number of morphologically distinct facial signals produced
82 by chimpanzees (using chimpFACS). According to this information, we predict that gibbons
83 would display a greater number of facial movements and have more complex signals than
84 chimpanzees. Gibbons and chimpanzees also exhibit differences in the proportion of slow-twitch
85 muscle fibers within their faces (Burrows et al., 2014; 2016). Compared to humans (*Homo*

86 *sapiens*), chimpanzees show a smaller proportion of slow-twitch facial muscle fibers (Burrows et
87 al., 2014). In contrast, gibbons have a proportion of slow-twitch facial muscles which falls in
88 between the human and chimpanzee range (Burrows et al., 2016).

89 In addition, apes (including humans, chimpanzees, and gibbons) possess a superficial
90 musculo-aponeurotic system (SMAS) between the skin and periosteum, with chimpanzees
91 exhibiting a quantitative reduction in subcutaneous connective tissue compared to humans
92 (Burrows et al., 2016). Gibbons, along with rhesus macaques (*Macaca mulatta*), demonstrate
93 subcutaneous connective tissue that falls between the range of humans and chimpanzees, with a
94 greater amount of connective tissue being observed between the dermis and zygomaticus major
95 muscle fibers than chimpanzees but less than humans (Burrows et al., 2016). The SMAS serves
96 as an anchor for mimetic muscles which are responsible for producing movement of the face
97 during bouts of communication. Having a robust SMAS is believed to be associated with greater
98 facial mobility (Burrows et al., 2016). Thus, the evidence and ideas behind the SMAS align with
99 evidence and ideas behind the facial muscle movements: both lead to the prediction that gibbons
100 should have larger and more complex signaling repertoires than chimpanzees.

101 *Social Behavior*

102 Gibbons and chimpanzees also vary greatly in their social behavior and organization.
103 Gibbons typically live in smaller social groups, comprising 2 to 6 individuals (Ryne, 1996). In
104 contrast, chimpanzees live in much larger groups, typically comprising 15 to 150 individuals
105 (Campbell et al., 2010). Gibbons are socially monogamous apes (instances of extra-pair
106 copulations have been documented; Reichard, 1995) whereas chimpanzees are polygamous.
107 Chimpanzees, unlike gibbons, exhibit a fission-fusion social structure where the size and
108 composition of subgroupings vary over time (Aureli et al., 2008; Sueur et al., 2011; Matthews,

109 2021), engage in group-level social activities (such as cooperative hunting; Boesch & Boesch,
110 1989), and learn complex behavioral patterns from other members of their social group (such as
111 tool use; (Lonsdorf, 2006). During these social interactions, chimpanzees produce a variety of
112 stereotyped facial signals not seen in gibbons. One example is lipsmacking, which has been
113 observed in affiliative interactions among chimpanzees (Pereira et al., 2020) but not in gibbons
114 (such as *Symphalangus syndactylus*; Liebal et al., 2004). However, in recent years a similar
115 stereotyped facial signal (referred to as a quiver) has been observed in white-handed gibbons
116 (*Hylobates lar*; Terleph et al, 2018). Differences in ecological (such as food availability) and
117 historical variables (such as time as an established pair/group) can also influence the social
118 behavior and organization of both apes (Thierry, 2013).

119 *Hypotheses*

120 Gibbons and chimpanzees both exhibit differences in their facial anatomy and social
121 behavior, making them ideal subjects for testing the *facial mobility hypothesis* and the *socio-*
122 *ecological complexity hypothesis*. The *facial mobility hypothesis* states that gibbons will have
123 larger and more complex facial signaling repertoires because they exhibit a greater number of
124 individual facial muscle movements (Waller et al., 2012) and a greater proportion of slow-twitch
125 muscle fibers (Burrows et al., 2014; Burrows et al., 2016) compared to chimpanzees. The
126 hypothesis is that primates (such as gibbons) who produce many documented facial muscle
127 movements will also combine these movements into numerous novel combinations (or facial
128 signals). In addition, more facial muscle movements and a greater proportion of slow-twitch
129 muscle will allow for more complex facial signals (where a signal can possess a greater number
130 of individual movements) due to increased motor control.

131 In contrast, the socio-ecological complexity hypothesis states that chimpanzees will have
132 larger and more complex facial signaling repertoires because they live in larger social groups
133 than gibbons. Many mammals use facial signals as reliable predictors of future behavior, such as
134 crested macaques (*Macaca nigra*; Waller et al., 2016), pigs (*Sus domesticus*; Camerlink et al.,
135 2018), capuchin monkeys (*Cebus apella*; Morimoto & Fujita, 2012), Bornean orangutans (*Pongo*
136 *pygmaeus*; Buttelmann et al., 2009), gorillas (*Gorilla gorilla*; Buttelmann et al., 2009), bonobos
137 (*Pan paniscus*; Buttelmann et al., 2009), and chimpanzees (*Pan troglodytes*; (Buttelmann et al.,
138 2009). Individuals may be able to increase the accuracy of their predictions or predict novel
139 social behaviors by increasing the size and complexity of their communicative repertoires. This
140 fine-tuned predictive framework could then be used to manage multiple social relationships
141 simultaneously and navigate complex social bond management activities (Whiten, 1997; Silk,
142 2002; Roberts & Roberts, 2019), which are often features of chimpanzee social groups.

143 *Predictions*

144 Our goal was to test the *facial mobility hypothesis* and the *socio-ecological complexity*
145 *hypothesis* by studying the facial behavior of gibbons and chimpanzees. These two hypotheses
146 have yet to be empirically tested since previous studies have not yet documented the number of
147 morphologically distinct facial signals observed in chimpanzees. For each hypothesis, we
148 generated the following predictions (which are also outlined in Table 1):

149 (1) The facial mobility hypothesis states that signal number and complexity are based on
150 the underlying mobility of the face. Therefore, we predicted (prediction 1A) that gibbons will
151 have a larger repertoire size than chimpanzees because gibbons can produce more facial
152 movements (i.e., facial action units) and have a greater proportion of slow-twitch facial muscles.
153 We also predicted (prediction 1B) that gibbon facial signals will be more complex than

154 chimpanzees, with complexity defined as the number of facial muscle movements used to make
155 a signal.

156 (2) The socio-ecological complexity hypothesis states that species living in larger social
157 groups should have larger repertoires and more complex signals than species living in smaller
158 social groups. Accordingly, we predicted (prediction 2A) that chimpanzees will have a greater
159 number of morphologically distinct facial signals documented than gibbons. We also predicted
160 (prediction 2B) that chimpanzees' facial signals would be more complex (i.e., consist of more
161 facial muscle movements) than gibbons to manage their larger number of interactions.

162 *TABLE 1. A brief description of our two hypotheses and their corresponding predictions.*

Hypothesis	Predictions
The Facial Mobility Hypothesis	1A. Gibbons will have a larger facial repertoire size than chimpanzees.
	1B. Gibbon facial signals will be more complex than those produced by chimpanzees.
The Socio-Ecological Complexity Hypothesis	2A. Chimpanzees will have a larger facial repertoire size than gibbons.
	2B. Chimpanzee facial signals will be more complex than those produced by gibbons.

163

164 To examine variation in facial mobility and facial signaling repertoires, we made use of
165 Facial Action Coding Systems (or FACSs) specifically designed for chimpanzees (Vick et al.,
166 2007) and gibbons (Waller et al., 2012). The first FACS was initially developed by Ekman &
167 Friesen in 1978 for humans and has been expanded upon to include non-human animals (Waller
168 et al., 2020). With FACS, individual muscle movements are assigned numerical codes, and the
169 combination of these numerical codes is used to reference a distinct facial signal. Facial muscle
170 movements which are shared among species are assigned the same numerical codes, making it

171 possible to conduct cross-species comparisons (Waller et al., 2020). FACS focuses exclusively
172 on facial muscle movements and does not attempt to ascribe subjective meaning to movements
173 or signals. The FACS uses video footage as opposed to anatomical illustrations to train its users
174 to identify subtle and overt facial muscle movement (Ekman and Rosenberg 2005). FACSs are
175 argued to be the most systematic and standardized method of studying human facial expressions
176 because they limit observation bias by placing equal emphasis on all facial muscle movements
177 (Parr et al., 2010). While multiple studies have examined facial mobility in primates using
178 FACSs (Parr et al., 2007; Scheider et al., 2014; Scheider et al., 2016; Florkiewicz et al., 2018),
179 they tend to focus on a single species or set of closely related species. There are two previous
180 studies which involved making cross-species comparisons with FACS (with *Canis lupus*
181 *familiaris* and *Pan troglodytes*), but both involved comparing the facial signaling behavior of
182 non-human animals to humans (Parr et al., 2007; Caeiro et al., 2017). Our study is the first to
183 draw comparisons between multiple non-human primate species.

184 To date, only three gibbon studies have reported on the extent of variation in facial
185 muscle movement combinations produced during bouts of communication using FACSs
186 (Scheider et al., 2014; Scheider et al., 2016; Florkiewicz et al., 2018). We make use of data from
187 two of these studies (Florkiewicz et al., 2018; Scheider et al., 2014), along with newly collected
188 chimpanzee data, to examine whether there are differences in the production of individual facial
189 muscle movements and facial muscle movement combinations between gibbons and
190 chimpanzees.

191 **METHODS**

192 We report how we determined our sample size, all data exclusions (if any), all
193 manipulations, and all measures in the study (below). This study was approved by the Los

194 Angeles Zoo, the Gibbon Conservation Center, Zoo Zurich, the Twycross Zoo, Howletts Wild
195 Animal Park, the Mulhouse Zoo, and NaturZoo Rheine. We followed the Animal Behavior
196 Society's Guideline for the Use of Animals. This study also adhered to the American Society of
197 Primatologists Principles for the Ethical Treatment of Non-Human Primates. Because our study
198 made use of non-invasive behavioral observations (which were recorded in visitor viewing
199 areas), full IACUC approval was waived for this study.

200 **Data Collection with Chimpanzees**

201 We collected data at the Los Angeles Zoo from 2017 to 2019 with a single troop of
202 chimpanzees (*Pan troglodytes*). We observed a total of 18 chimpanzees throughout the study.
203 We collected data Monday through Friday from 8:00 to 14:00, which we identified as peak
204 activity hours during a pilot study in 2016. We used two different sampling methods to gather
205 our data: the focal individual sampling method (which took place in 2017; (Altmann, 1974) and
206 the opportunistic sampling method (which took place from 2018 to 2019; (Florkiewicz &
207 Campbell, 2021). For the focal individual sampling method, we recorded each troop member in
208 30-minute intervals, with each individual sampled once per week. We randomized the order and
209 time in which we recorded individuals. The focal individual sampling method resulted in 72
210 hours of video footage (or 4 hours per individual). For the opportunistic sampling method, we
211 followed the most active portion of the troop and recorded all social interactions. We began
212 recordings just before the start of a social interaction and ended them when chimpanzees
213 dispersed and/or ceased their communication. Our video recordings varied in length based on the
214 duration of social interaction(s). The opportunistic sampling method resulted in 84.5 hours of
215 video footage. We combined data across the two methods since our previous comparison of the

216 sampling methods showed that they performed similarly (Florkiewicz & Campbell, 2021). When
217 combined, these sampling methods resulted in 156.5hr of footage for chimpanzees.

218 **Data Collection with Gibbons**

219 We used previously recorded video footage which spanned five different institutions.
220 Data collection in Scheider et al. (2014) took place at the Twycross Zoo (N=6 individuals), the
221 Zurich Zoo (N=4), the Mullhouse Zoo (N=4), and the Rheine Zoo (N=2). The 16 individuals
222 represented five different species: *Symphalangus syndactylus* (N=6), *Hylobates pileatus* (N=4),
223 *Hylobates lar* (N=2), *Nomascus gabriellae* (N=2), and *Nomascus siki* (N=2). Data collection in
224 Florkiewicz et al. (2018) took place at the Gibbon Conservation Center comprising 20
225 individuals across 4 species: *Hylobates moloch* (N=6), *Hylobates pileatus* (N=2), *Hoolock*
226 *leuconedys* (N=8), and *Nomascus leucogenys* (N=2). In total, our analysis includes 36
227 individuals from 8 species and all 4 genera of Hylobatids. Both studies used the focal pair
228 sampling method to continuously video record the subjects (Altmann, 1974). We collected a total
229 of 227hr of footage between the two studies; 21hr in Scheider et al. 2014, and 206hr in
230 Florkiewicz et al. 2018.

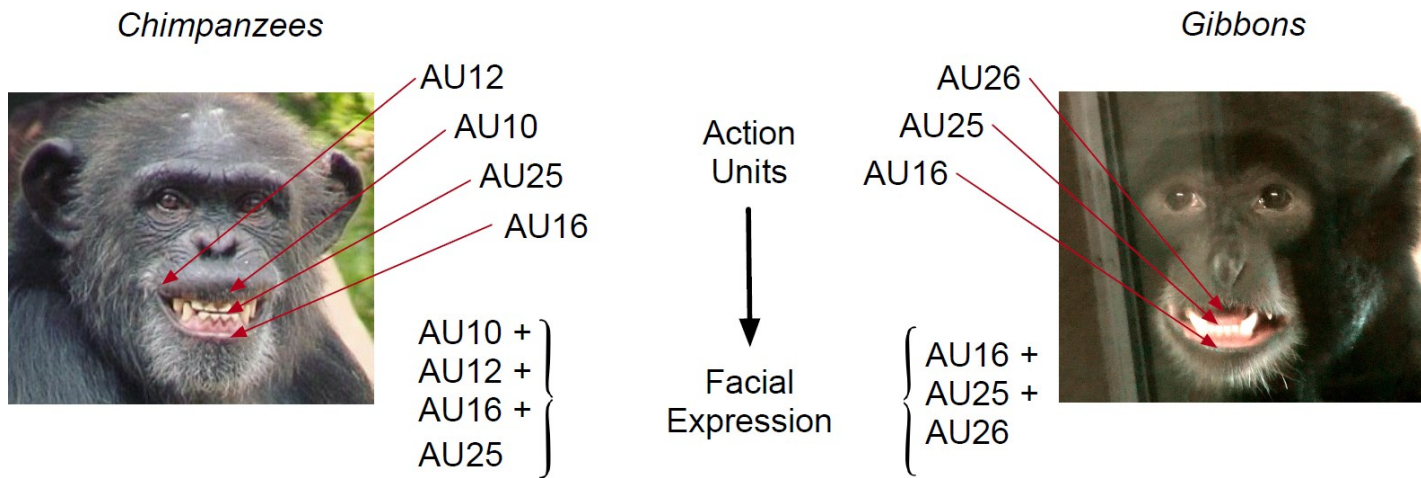
231 Information regarding the names, age groups, birthplaces and sexes of the chimpanzees
232 and gibbons incorporated into this study can be found in the electronic supplement (Table S1).

233 **Data Coding**

234 In the current study, we defined a *facial signal* as a facial muscle movement that a
235 signaler performs during bouts of communication to the potential recipient(s), based on the
236 broader definition of a communicative signal (Smith & Harper, 1995). Our definition of a facial
237 signal does not include facial muscle movements which are exclusively used for biological

238 maintenance (such as blinking, mastication, breathing, etc.). We did not include head movements
 239 in the current study, since it is difficult to discern whether they are communicative in nature.
 240 Each facial signal can consist of one or more facial muscle movements, defined as the
 241 contraction and/or relaxation of muscles on the face (i.e., above the neck region). Each facial
 242 signal we identified was coded using Facial Action Coding Systems (or FACSs). Following from
 243 the ChimpFACS and GibbonFACS tools, we referred to each facial muscle movement as an
 244 action unit (or AU), and we assigned each facial signal a numerical combination (or AU
 245 combination; (Ekman & Rosenberg, 2005), see Figure 1).

246



247

248 *FIGURE 1. A visual representation of how to code facial signals using FACS. Single*
 249 *muscle movements (which are referred to as Action Units or AUs) are used in combination*
 250 *leading to facial movement combinations (AU combinations). Photo credit: chimpanzee photo by*
 251 *Britt Florkiewicz (left); siamang photo from the GibbonFACS Manual (© Manuela Ersson-*
 252 *Lembeck). The following AUs were included in this figure: AU10 (Upper Lip Raiser), AU12 (Lip*
 253 *Corner Puller), AU16 (Lower Lip Depressor), AU25 (Lips Part), and AU26 (Jaw Drop).*

254

255 We coded all chimpanzee facial signals using the ChimpFACS (Vick et al., 2007), and
256 we coded gibbon facial signals using the GibbonFACS (Waller et al., 2012). Microsoft Excel
257 was used for GibbonFACS coding, and ELAN 5.6-AVFX (with a custom coding template) was
258 used for ChimpFACS coding. Additional information about the AUs documented in the
259 ChimpFACS and GibbonFACS can be found in the electronic supplement (Table S2).

260 **Inter-Observer Reliability (IOR)**

261 We assessed agreement using Wexler's Ratio, a common practice in studies that use
262 FACSs (Parr et al., 2007). The equation for Wexler's ratio is: $[2 * (\# \text{ of AUs Agreed on by Both}$
263 $\text{ Coders})] / [(\# \text{ of AUs coded by R1}) + (\# \text{ of AUs coded by R2})]$, with R1 denoting researcher 1 and
264 R2 denoting researcher 2 (Parr et al., 2007). We calculated Wexler's ratio for each facial signal
265 with the average ratio used to assess agreement. We used a minimum Wexler's ratio of 0.70 for
266 'good' agreement, a standard threshold for passing human and non-human FACSs certification
267 tests (Lewinski et al., 2014). We performed IOR on a subset of facial signaling data in each
268 study. Both Scheider et al. (2014) and Florkiewicz et al. (2018) calculated agreement for 10% of
269 observed facial signals. Scheider et al. (2014) reported an average Wexler's ratio of 0.83, and
270 Florkiewicz et al. (2018) reported an average Wexler's ratio of 0.73. Chimpanzee AU
271 combinations had an average Wexler's ratio of 0.75. As all the ratios are above the 0.70
272 threshold, we considered them all to be in good agreement. All researchers that were recruited to
273 perform IOR were blind to the aims of the current study.

274 **Data Analysis**

275 We performed statistical tests in R 3.6.2 (R Core Team 2017). Our combined behavioral
276 data and R code can be found in the electronic supplement. To test the *facial mobility hypothesis*
277 and *socio-ecological complexity hypothesis*, we compared chimpanzees and gibbons regarding
278 the morphology and complexity of their facial signals. According to the *facial mobility*
279 *hypothesis*, we predicted that gibbons would have: (1A) a greater number of morphologically
280 distinct facial signals; and (1B) signals with a larger number of action units than chimpanzees.
281 According to the *socio-ecological complexity hypothesis*, we predicted that chimpanzees would
282 have: (2A) a greater number of morphologically distinct facial signals; and (2B) signals with a
283 larger number of action units than gibbons.

284 In the current study, we draw comparisons between apes (*Pan troglodytes* and family
285 Hylobatidae) rather than species for two main reasons. Most gibbon species exhibit similarities
286 in their social behavior and organization (Gittins, 1980; Southwick, 1985; Ryne, 1994; Campbell
287 et al., 2010), and previous studies have identified consistency in facial signaling behavior across
288 gibbon species (Scheider et al., 2014; Florkiewicz et al., 2018). In addition, previous studies have
289 found no relationship between facial signaling behavior (in the form of rates, repertoire
290 composition, and diversity of repertoires) and socio-ecological factors across gibbons, such as
291 group size and extent of monogamy (Scheider et al., 2014). Similar facial signaling behavior
292 across gibbons may be attributed to similarities in their overall socio-ecology.

293 We faced two challenges in our analysis. First, there were differences in the number of
294 hours recorded for each ape and species across the three studies. As a whole, we had more hours
295 for gibbons (N=227hr) than chimpanzees (N=156.5hr). Some species (such as *Nomascus*
296 *gabriellae*) were only sampled in one study ((Scheider et al., 2014); N=2.5hr), whereas others
297 were sampled in two studies (Table S1). Second, there could be idiosyncratic variation in facial

298 signaling behavior. Our current study includes data from 54 individuals: 36 gibbons and 18
299 chimpanzees. Some AUs or AU combinations may be restricted to certain individuals, especially
300 those who are seldom observed. It is also possible that other factors, such as age and sex
301 contribute to differences in facial signaling behavior. If unaccounted for, these differences could
302 impact our analyses pertaining to the diversity and complexity of facial signals in chimpanzees
303 and gibbons.

304 To account for differences in recording time and idiosyncrasies and between apes, we
305 used: (1) corrected repertoire sizes; and (2) generalized linear mixed models. Corrected facial
306 repertoire sizes (R_{CM}) were first introduced by Scheider et al. (2014) as a method to account for
307 differences in recording time between species. To calculate R_{CM} in our current study, we divided
308 the number of AU combinations observed for each ape type by their recording time (in minutes).
309 We then compared our R_{CM} scores using a two-sample test for equality. By using corrected
310 repertoire sizes, we were able to make direct comparisons between chimpanzees and gibbons to
311 test predictions 1A and 2A. To account for both idiosyncratic differences and differences in
312 recording time, we also used generalized linear mixed models (or GLMMs). GLMMs help to
313 account for the pooling fallacy and idiosyncratic differences in signaling behavior through
314 random effects (Waller et al., 2013). By using an offset term, we can also account for differences
315 in recording time across species.

316 We ran three different sets of models to examine differences in: (M1) the use of
317 individual AU's; (M2) the use of AU combinations; and (M3) the complexity of facial signals
318 (i.e., the number of AUs that are produced in a given facial signal). We used model sets M1 and
319 M2 to examine differences in facial signaling morphology (i.e., test predictions 1A and 2A),
320 whereas we used models in set M3 to examine differences in facial signaling complexity (i.e.,

321 test predictions 1B and 2B). For all of our models, we set signaler ID as a random variable to
322 help account for idiosyncratic differences in facial signaling behavior. We also used an offset
323 term to account for differences in recording time (in minutes) across the nine species.

324 *Facial Signaling Morphology Models (M1 and M2)*

325 To make comparisons between chimpanzees and gibbons facial signaling morphology,
326 we analyzed facial signals at two different levels: (1) the AU; and (2) the AU combination. This
327 is because each facial signal (i.e., AU combination) comprises multiple facial muscle movements
328 (i.e., AUs). Chimpanzees and gibbons may differ in the production and use of AUs, which could
329 impact the composition of their AU combinations. To account for differences in the production
330 of AUs and AU combinations, we ran two sets of models.

331 In the first set of models (M1 series), we selected the number of observations per AU as
332 the outcome variable. For model set M1, we tested five different models, containing a
333 combination of four different explanatory variables. In the first model (M1.1), we set ape type as
334 an explanatory variable to determine whether there are significant differences in the production
335 of AUs and AU lengths between gibbons and chimpanzees. In the second model (M1.2), we
336 examined the interaction between categories of AUs and AU lengths with ape type to better
337 understand why gibbons and chimpanzees are similar/different from one another. In the
338 remaining three models, we included age (M1.3), sex (M1.4), and a combination of both (M1.5)
339 as explanatory variables in addition to our interaction term. For our M1 series, we ran Negative-
340 Binomial GLMMs (NB-GLMMS) since our outcomes were discrete counts of each AU
341 observed, and the variance was greater than the mean.

342 In the second set of models (M2 series), we set the number of observations per AU
343 combination as the outcome variable. We followed a similar procedure as the M1 series for our
344 M2 model set, which examines differences in gibbons and chimpanzees in the production of AU
345 combinations. However, we did not include an interaction between ape type and AU
346 combination type for two main reasons: (1) there were a large number of AU combinations
347 identified across apes (N=65); and (2) the data were zero-inflated, which led to convergence
348 issues when including interaction terms. For model M2.1, we included ape type as an
349 explanatory variable. In the remaining four models, we included age (M2.2), sex (M2.3), and a
350 combination of both (M2.4) as explanatory variables in addition to ape type. In our AU
351 combination dataset, approximately 84.9% of all data points had a value of 0 assigned for the
352 outcome variable, resulting in a zero-inflated dataset resembling a negative-binomial
353 distribution. To accommodate this, we used Zero-Inflated Negative-Binomial GLMMs (ZINB-
354 GLMM).

355 *Facial Signaling Complexity Models (M3)*

356 We defined *complexity* as the number of AUs used to produce a given AU combination
357 (i.e., more AUs = more complexity). For example: AU25+AU26 is comprised of two distinct
358 AUs and would be considered less complex than AU combinations with 3 or more AUs (such as
359 AU16+AU25+AU26). After coding all facial signals observed with the chimpFACS and the
360 gibbonFACS, we counted the number of AUs used to produce each facial signal (or AU
361 combination). We used this information to construct our categorical outcome variable “AU
362 Length.” Initially, we had seven categories associated with AU Length (with AU combinations
363 ranging in length from 1 to 7 AUs). However, we had a small number of facial signaling
364 observations, which consisted of 7 AUs (N=3), so we removed this category from our analyses.

365 For model M3.1, we included ape type as an explanatory variable. In the remaining four models,
366 we included age (M3.2), sex (M3.3), and a combination of both (M3.4), in addition to ape type.
367 For our M3 series, we ran Ordinal GLMMs (O-GLMMS) since our outcome variable (AU
368 Length) consisted of naturally ordered (based off of the number of AU's present within a given
369 AU Combination, with each step above the previous consisting of +1 AUs).

370 *Model Selection Procedure*

371 We compared and selected the best-fitting models for each model series using Akaike's
372 Information Criterion (or AIC) scores. To compare our models, we calculated the difference
373 (ΔAIC) between each model i (AIC_i) and the model with the lowest AIC score l (AIC_l ;
374 Preininger et al., 2013). We considered models with an ΔAIC value of ≤ 2 to be good fitting
375 models, and we considered the model with the lowest ΔAIC to be the best-fitting model
376 (Preininger et al., 2013). AIC and ΔAIC scores for all models can be found in the electronic
377 supplement (Table S3).

378 Our best-fitting models were M1.3 (ApeType*AU + Age), M2.1 (ApeType), and M3.1
379 (ApeType). For our M1 series, models M1.3 and M1.5 had matching scores for both AIC and
380 ΔAIC . Therefore, we went with the simpler model (M1.3: ApeType*AU + Age) since adding the
381 variable sex in M1.5 did not significantly improve the fit of the model (which would result in a
382 lower AIC and ΔAIC than M1.3). We will discuss these models in our results section, and their
383 outputs can be found in the electronic supplement. For our best-fitting models, explanatory
384 variables were only considered to be significant if $p < 0.05$. For M1.3, we separated the data into
385 smaller subsets (based on AU category) to calculate significant effects (Preininger et al., 2013)
386 for our interaction term (ApeType*AU). This allowed us to determine whether there were
387 significant effects for each AU between apes. We also performed pairwise comparisons to

388 examine differences between the four age groupings in model M1.3. For model 3.1, we
389 conducted two-sample tests for equality of proportions to determine the source of significance
390 between thresholds.

391 To run model sets M1 and M2 in R, we used the packages “r2admb” and “glmmADMB,”
392 which run both zero-inflated and non-zero-inflated negative-binomial GLMMs (Fournier et al.,
393 2012). To run model set M3, we used the package “ordinal,” which is specifically designed to
394 run ordinal GLMMs (Christensen, 2019). We calculated AIC and Δ AIC scores for all our models
395 using the package ‘bbmle’ (Bolker, 2021). Our datasets, R code, and outputs for the remaining
396 models can be found in the electronic supplement.

397 **RESULTS**

398 After combining datasets, we observed a total of 9,140 facial signaling events (N=1,091
399 for chimpanzees; N=8,049 for gibbons) across 383.5hr of video footage (N=156.5hr for
400 chimpanzees; N=227hr for gibbons). These 9,149 facial signals include communicative signals
401 only, and do not represent non-communicative movements associated with biological
402 maintenance. Initially, we identified a total of 37 distinct AUs and 432 distinct AU
403 combinations. Out of the 37 muscle movements observed, we observed 22 in gibbons and 27 in
404 chimpanzees. Out of the 432 AU combinations observed, we observed 80 in gibbons and 357 in
405 chimpanzees. Our initial results suggest that chimpanzees produce a greater variety of AUs and
406 AU combinations. However, this could be attributed to differences in use, visibility, and/or study
407 design. For example, chimpanzees and gibbons can produce AU1+2 (inner and outer brow
408 raiser), but we only observed this movement in gibbons. It is unclear if this is attributed to
409 differences in use (i.e., that gibbons use AU1+2 for communication, whereas chimpanzees do
410 not) or in reduced visibility with our chimpanzee video footage. To account for these

411 possibilities, we decided to take a conservative approach and focus only on AUs identified across
412 all three studies. We removed all other AUs from our combined dataset. We will focus on this
413 filtered dataset for the rest of our results. The original and modified datasets can be found in the
414 electronic supplement.

415 **Facial Signaling Morphology**

416 In our filtered dataset, we observed a total of 5,521 facial signaling events (N=1,068 for
417 chimpanzees; N=4,453 for gibbons). We identified a total of 12 distinct AUs shared between
418 chimpanzees and gibbons. These 12 distinct AUs were used by apes to produce 65 distinct AU
419 combinations.

420 *AU Combinations*

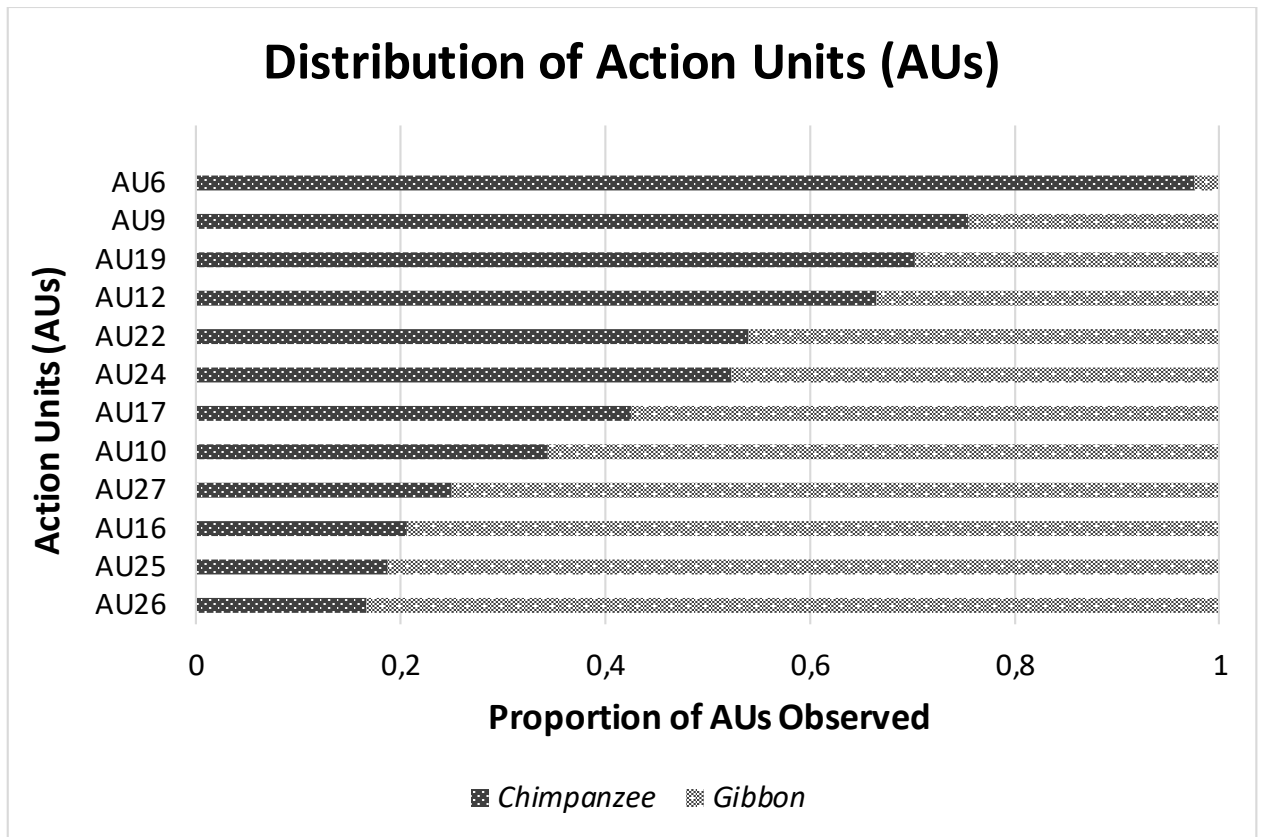
421 Out of the 65 distinct AU combinations observed, we found 21 in both gibbons and
422 chimpanzees, 14 AU combinations exclusive to gibbons, and 30 AU combinations exclusive to
423 chimpanzees. After accounting for differences in recording time between apes, we found that
424 chimpanzees have a significantly larger corrected repertoire size (R_{CM}) than gibbons ($\chi^2=12.563$,
425 $p=0.003$). Our best fitting model only contained ape type as a fixed explanatory variable
426 (AIC=5665.04; $\Delta AIC=0.0$); the incorporation of age and/or sex as fixed variables reduced the fit
427 of our model ($\Delta AIC=1.4-6.5$). Our ZINB-GLMM revealed that differences in the production of
428 AU combinations between chimpanzees and gibbons are significant ($\beta=2.173$; $SE=0.361$;
429 $z=6.020$; $p<0.001$).

430 We found that differences in the production of AU combinations for each ape (with
431 production being associated with the number of unique AU combinations and number of

432 observations per AU combination) appear to be associated with differences in: (1) the production
433 of individual AUs; and (2) the production of complex facial expressions.

434 *Action Units (AUs)*

435 Our best fitting NB-GLMM revealed moderate differences regarding the overall
436 production of AUs between chimpanzees and gibbons ($\beta=0.878$; $SE=0.516$; $z=1.700$; $p=0.089$).
437 There were significant differences between chimpanzees and gibbons in the production of the
438 following AUs: AU6 ($\beta= -3.036$; $SE=0.788$; $z=-3.860$; $p<0.001$), AU10 ($\beta=1.234$; $SE=0.509$;
439 $z=2.430$; $p=0.015$), AU16 ($\beta=2.035$; $SE=0.518$; $z=3.93$; $p<0.001$), AU25 ($\beta=2.863$; $SE=2.99$;
440 $z=9.58$; $p<0.001$), AU26 ($\beta=2.912$; $SE=0.297$; $z=9.820$; $p<0.001$), and AU27 ($\beta=1.508$;
441 $SE=0.506$; $z=2.980$; $p=0.003$). Chimpanzees produced significantly more AU6's, whereas
442 gibbons produced significantly more AU10's, AU16's, AU25's, AU26's, and AU27's (Figure 2).
443 There were no significant differences in the production of AU12, AU17, AU19, AU22, AU24,
444 and AU9 ($p>0.05$). While our best fitting model included age category as a predictor variable
445 ($AIC=3786.90$; $\Delta AIC=0.0$), there were no significant differences in the production of AUs
446 between infants, subadults, and adults; however, there were significant differences between
447 juveniles and adults (Pair-wise comparison: $\beta=2.206$; $SE=0.771$; $z=2.863$; $p=0.019$).



448

449 *FIGURE 2. A stacked histogram chart showing the proportion of observations (x-axis) for each*
 450 *AU type (y-axis) across chimpanzees and gibbons.*

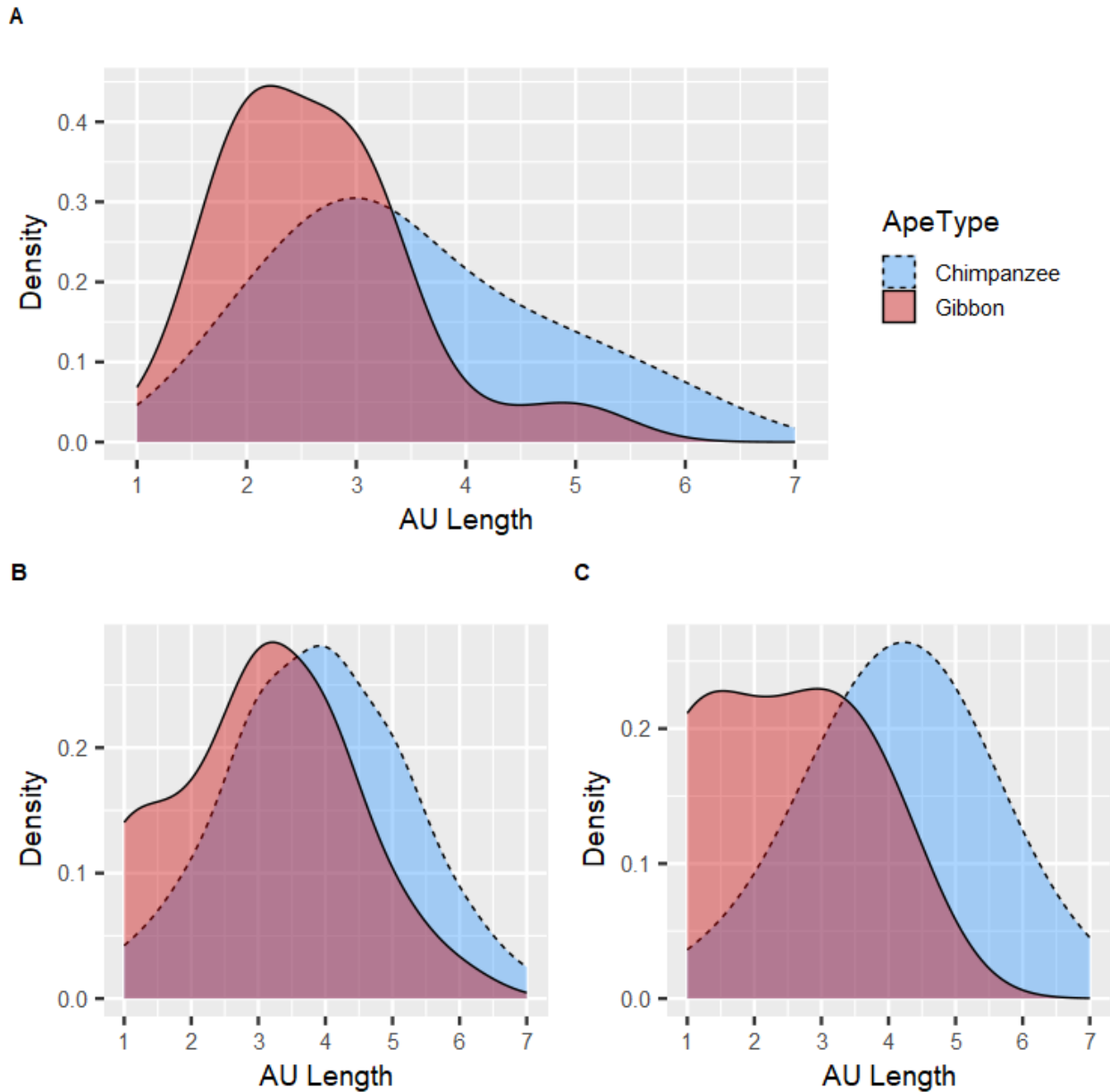
451 Differences in the number of AUs produced by each ape can partially explain differences
 452 in the production of AU combinations for each ape. For example, chimpanzees produced
 453 significantly more AU6's compared to gibbons. As a result, chimpanzees produced AU
 454 combinations that contained AU6 more frequently (N=84) than gibbons (N=2). Interestingly, out
 455 of the 30 AU combinations unique to chimpanzees, 8 contained AU6. Only 1 of the 14 unique
 456 AU combinations observed in gibbons contained AU6. However, this pattern was not consistent
 457 across AUs and apes. For example: gibbons produced significantly more AU10's compared to
 458 chimpanzees ($\beta=1.234$; $SE=0.509$; $z=2.430$; $p=0.015$). As a result, gibbons produced AU
 459 combinations that contained AU10 more frequently (N=444) than chimpanzees (N=232). Out of

460 the 14 unique AU combinations observed in gibbons, 5 contained AU10. However, 10 of the 30
461 unique AU combinations observed in chimpanzees contained AU10. It appears that differences
462 in the complexity of chimpanzee and gibbon facial signals can also explain differences in the
463 production of AU combinations produced by each ape.

464 **Facial Signaling Complexity**

465 There was variation in the complexity of AU combinations, with complexity being
466 defined as the number of AUs used to produce an AU combination. Most AU combinations
467 observed (83.23%) consisted of either two (42.57%) or three (40.66%) AUs. It was less common
468 to observe AU combinations consisting of four or more AUs (15.02%). It was also rare to
469 observe an AU combination consisting of a single AU (1.76%). For our O-GLMM, we compared
470 the number of facial signals observed in each level of complexity between chimpanzees and
471 gibbons (Figure 3A). Our best fitting model only contained ape type as a fixed explanatory
472 variable (AIC=11461.02; Δ AIC=0.0); the incorporation of age and/or sex as fixed variables
473 reduced the fit of our model (Δ AIC=1.2-2.9).

474



475

476 *FIGURE 3. Complexity of AU combinations in chimpanzees (blue dashed line) and gibbons (red*
 477 *continuous line). Complexity is defined as the number of unique AUs (x-axis) an AU combination*
 478 *is composed of. (A) Number of AUs associated with facial signals produced by chimpanzees and*
 479 *gibbons. (B) Number of AUs associated with AU combinations produced by chimpanzees and*
 480 *gibbons. This includes AU combinations that are shared between apes and are unique to each*

481 *ape. (C) Number of AUs associated with AU combinations that are unique to either chimpanzees*
482 *or gibbons only.*

483 On average, chimpanzees produced more complex facial signals (mean=3.49, standard
484 deviation=1.21) compared to gibbons (mean=2.63, standard deviation=0.82). The results of our
485 O-GLMM show that ape type shows a trend for a moderate effect on facial signaling complexity
486 ($\beta=-0.627$; SE=0.378; $z=-1.658$; $p=0.0974$). For gibbons, the odds of producing a more complex
487 facial signal (i.e., one which consists of 2 or more AUs) is 46.57% lower than for chimpanzees
488 (OR=0.534; CI=0.255-1.121). To better understand why ape type only had a moderate effect on
489 facial signaling complexity, we ran a 2-sample test for equality of proportions for each level of
490 facial signaling complexity. We found that gibbons produce a significantly greater proportion of
491 facial signals with 1 AU ($\chi^2=10.063$, $p=0.002$), 2 AUs ($\chi^2=256.27$, $p<0.001$), and 3 AUs
492 ($\chi^2=3.998$, $p=0.050$) than chimpanzees. In contrast, we found that chimpanzees produce a
493 significantly greater proportion of facial signals with 4 AUs ($\chi^2=368.74$, $p<0.001$), 5 AUs
494 ($\chi^2=88.652$, $p<0.001$), and 6 AUs ($\chi^2=336.74$, $p<0.001$) than gibbons.

495 Differences in the complexity of facial signals produced by each ape can also explain
496 differences in the production of AU combinations for each ape (Figure 3B & 3C). The
497 complexity of AU combinations is similar across both apes when considering all AU
498 combinations that they produce (which includes AU combinations that are shared among both
499 apes and are also novel to each ape; Figure 3B). However, when examining the complexity of
500 AU combinations that are exclusive to each ape type, interesting patterns emerge (Figure 3C). Of
501 the 30 AU combinations unique to chimpanzees, 21 contained 4 or more AUs. Only 3 of the 14
502 unique AU combinations observed in gibbons contained 4 or more AUs. In contrast, out of the
503 14 unique AU combinations observed in gibbons, 11 contained 1-3 AUs. Only 9 out of the 30

504 unique AU combinations produced by chimpanzees contained 1-3 AUs. Additional information
 505 regarding AU combinations and corresponding AU Lengths for both apes can be found in the
 506 supplemental materials.

507 **DISCUSSION**

508 The goal of our current study was to compare how facial signals are shaped by anatomy
 509 and social structure between distantly related apes. Specifically, we tested two hypotheses: (1)
 510 the *facial mobility hypothesis* (predictions 1A and 1B); and (2) the *socio-ecological complexity*
 511 *hypothesis* (predictions 2A and 2B; see Table 2).

512 *TABLE 2. A brief description of our two hypotheses, their corresponding predictions,*
 513 *whether these predictions were supported, and how we analyzed the evidence.*

Hypothesis	Predictions	Support	Evidence
The Facial Mobility Hypothesis	1A. Gibbons will have a larger facial repertoire size than chimpanzees.	No	R _{CM} , ZINB-GLMMs, NB-GLMMs
	1B. Gibbon facial signals will be more complex than those produced by chimpanzees.	No	Ordinal GLMMs, Two-sample test for equality
The Socio-Ecological Complexity Hypothesis	2A. Chimpanzees will have a larger facial repertoire size than gibbons.	Yes	R _{CM} , ZINB-GLMMs, NB-GLMMs
	2B. Chimpanzee facial signals will be more complex than those produced by gibbons.	Yes	Ordinal GLMMs, Two-sample test for equality

514

515 We found that chimpanzees produced a greater variety of AUs (i.e., facial muscle
 516 movements) and AU combinations than gibbons (Figure 3), which provides support for
 517 prediction 2A and evidence against prediction 1A (Table 2). To verify that these results were not
 518 due to differences in coding schemes and/or differences in video quality, we ran a further
 519 analysis on only the AUs identified and shared across chimpanzees and gibbons. The pattern
 520 remained in this filtered sample: chimpanzees produced a greater variety of AU combinations
 521 than gibbons despite having fewer recording hours, fewer individuals sampled, and fewer facial

522 signaling observations. Chimpanzees also produced facial signals which were more complex on
523 average (i.e., consisted of a greater number of AUs) than those observed in gibbons, supporting
524 prediction 2B and opposing prediction 1B (Table 2). Our results suggest that having increased
525 facial mobility does not necessarily lead to large and more complex facial signaling repertoires.
526 Rather, social structure and the number of possible interactions appears to drive a greater number
527 of AUs used and combined into signals.

528 While chimpanzees have larger and more complex facial signaling repertoires than
529 gibbons, both chimpanzees and gibbons still exhibit similarities in their facial signaling
530 morphology. Our current study focused on 12 AUs, which we observed in both chimpanzees and
531 gibbons. These 12 AUs were used to produce 21 AU combinations in both chimpanzees and
532 gibbons. The presence of shared AUs and AU combinations may well be the result of
533 evolutionary continuity. Many of the AUs found in both chimpanzees and gibbons are also found
534 in a wide variety of mammals (Waller et al., 2020), such as orangutans (Caeiro et al., 2013),
535 macaques (Parr et al., 2010), marmosets (Correia-Caeiro et al., 2022), horses (Wathan et al.,
536 2015), dogs (Waller et al., 2013), and cats (Caeiro et al., 2013). This includes AU10, AU12,
537 AU16, AU25, AU26, and AU27 (Waller et al., 2020). These AUs are often used to produce
538 stereotyped facial signals found in various mammal species (Andrew, 1963). One example of
539 this can be seen with ‘threat’ displays. Threat displays are found in a wide variety of mammal
540 species and typically involve opening the mouth (AU25, AU26, and 27), drawing the corners of
541 the lips backward (AU12), and/or exposing both rows of teeth (AU10 and AU16; Andrew 1963).

542 However, the results of our study show that shared ancestry alone cannot explain facial
543 repertoire size and use. While chimpanzees and gibbons share 12 AUs, we discovered
544 differences in how they are produced and used by each ape. Chimpanzees produced significantly

545 more AU6's, whereas gibbons produced significantly more AU10's, AU16's, AU25's, AU26's,
 546 and AU27's. Differences in AU production could be attributed to differences in contextual use.
 547 For example, AU6 is often associated with the production of bared teeth faces in primates (Parr
 548 et al., 2007). While both chimpanzees and gibbons can produce bared teeth faces (Liebal et al.,
 549 2004; Parr et al., 2007), our study found that chimpanzees are significantly more likely to
 550 produce this AU. Previous studies have found that chimpanzees frequently use bared teeth to
 551 signal affiliation (Waller & Dunbar, 2005) and/or submissiveness (Van Hooff, 1967). In contrast,
 552 bared teeth faces are mostly produced by adult male gibbons in the context of sex (Liebal et al.,
 553 2004).

554 Unfortunately, contextual data were only available for one of our two gibbon datasets
 555 (Scheider et al., 2014). However, we do have contextual data for our chimpanzee dataset, which
 556 make it possible to draw some preliminary comparisons between the two ape types. When
 557 combining our newly acquired chimpanzee data and the gibbon data from Scheider et al. (2014),
 558 we have a total of 2,197 facial signals produced across 11 different contexts. This information
 559 can be found below in Table 3. There were some differences in the number of facial signals
 560 observed in each context for both chimpanzees and gibbons, which could have impacted the
 561 prevalence of certain AUs. For example: AU6 is often associated with affiliative/submissive
 562 contexts in chimpanzees, whereas in gibbons it is often associated with the context of
 563 reproduction. We observed very few facial signals being produced during reproductive contexts
 564 in gibbons (N=8), which could explain why chimpanzees produced significantly more AU6's.

565 *TABLE 3. A breakdown of the number of signals observed in each behavioral context for*
 566 *chimpanzees and gibbons (Scheider et al., 2014).*

Context	Chimpanzees	Scheider et al., 2014
---------	-------------	-----------------------

AFFILIATIVE	153	0
AGONISTIC	151	76
AROUSAL (GENERAL)	176	0
FOOD	62	0
GROOM	137	194
LOCOMOTION	52	0
Nursing	0	20
PLAY	325	144
REST	8	417
SEX	23	8
UNSURE/UNKNOWN	4	247
TOTAL	1091	1106

567

568 Chimpanzees also possess a larger and more complex facial signaling repertoire than
569 gibbons, supporting our *socio-ecological complexity hypothesis*. Compared to gibbons,
570 chimpanzees live in larger social groups, consisting of individuals who vary in age, sex, and
571 genetic relatedness (Southwick, 1985). Chimpanzees also exhibit a fission-fusion social
572 structure, where individuals break off into smaller subunits throughout the day (Aureli et al.,
573 2008). The size and composition of these smaller subunits vary based on social and ecological
574 factors, such as food availability and the presence of potential reproductive partners (Aureli et
575 al., 2008; Matthews, 2021). This form of social organization leads to a multilevel society where
576 relationships are established and maintained between individuals, dyads, subunits, and
577 neighboring groups (Prox & Farine, 2020). While there is variability in the quality (Florkiewicz
578 et al., 2018; Geissmann et al., 2020) and quantity (Barelli et al., 2013) of social relationships
579 among gibbons, most live in relatively small social groups consisting of one set of pair-bonded
580 individuals and their offspring (Ryne, 1994).

581 Differences in facial signaling function could explain differences in the size and
582 composition of facial signaling repertoires in both chimpanzees and gibbons. In chimpanzees,

583 having a large and complex facial signaling repertoire may be important for managing a larger
584 number of social relationships that vary in type, duration, and associated social behaviors (due to
585 fission-fusion dynamics). In gibbons, facial synchrony is essential for coordinating activities
586 needed to establish and maintain long-term pair bonds (Florkiewicz et al., 2018). One example of
587 synchronous activity in gibbons includes vocal duetting, where songs strengthen social bonds
588 and advertise territorial boundaries (Geissmann, 1993). However, this does not necessarily
589 suggest that chimpanzees do not exhibit facial synchrony or that gibbons are unable to maintain
590 multiple relationships with others. Facial synchrony (rapid and delayed facial mimicry) during
591 bouts of play in chimpanzees is important for modulating play sessions and communicating
592 playful motivations (Palagi et al., 2019). In gibbons, extra-pair copulations suggest that social
593 relationships can be established and maintained outside of the pair bond (Barelli et al., 2013).

594 The results of our study have important implications for the evolution of human facial
595 signaling. Many of the facial muscles and movements observed in gibbons and chimpanzees can
596 also be found in humans (Waller et al., 2020). Morphological changes to the human face (such as
597 the addition of new facial muscles, an increase in slow-twitch muscle fibers, and a superficial
598 musculo-aponeurotic system (SMAS); Ekman & Rosenberg, 2005; Burrows et al., 2014;
599 Burrows et al., 2016) could have resulted in larger and more complex facial signaling repertoires
600 when compared to nonhuman animals. However, changes in facial musculature and movement
601 could have been facilitated by changes in social organization. Similar to chimpanzees, humans
602 exhibit fission-fusion social dynamics and relatively large community sizes (Aureli et al., 2008).
603 But in contrast to chimpanzees, humans exhibit a greater degree of both spatial and temporal
604 cohesion of group members, with group sizes being significantly larger (Aureli et al., 2008).
605 Humans also exhibit different types of bonds (which includes social and economic relationships),

606 engage in greater alloparental investment, and have established complex trading networks
607 (Aureli et al., 2008). Hence, from gibbons to chimpanzees to humans we see a scaling up of both
608 social structure complexity and facial signaling complexity. The greater social demands could
609 have provided the selection pressure for more complex signaling repertoires. The anatomical
610 changes to produce more complex signals could have involved additions aimed at control (e.g.,
611 slow-twitch fibers, SMAS) and subtractions aimed efficiency (fewer total AUs). In other words,
612 the route to complex signals may involve more control over fewer units. Such changes could
613 explain why gibbons have a greater number of raw movements they can produce but fewer
614 complex combinations of those movements than chimpanzees. Ultimately, these changes could
615 have given rise to larger and more complex facial signaling repertoires, which may have also
616 been a key component in the evolution of language (coupled with changes in cognition and the
617 larynx; Nishimura et al., 2022).

618 **Study Limitations and Future Directions**

619 Our results support socio-ecology as playing an important role in the evolution of primate
620 facial signaling repertoires, but there are five limitations to our study that we have identified.
621 First, we mainly focused on AUs produced by both chimpanzees and gibbons. We took a
622 conservative approach to the study of these individual AUs since it was unclear if differences
623 between apes (in the production of certain AUs) were attributed to differences in usage or
624 methodological constraints between the three studies. Second, we only considered one of five
625 variables associated with the social complexity hypothesis (Freeberg et al., 2012). In this study,
626 we compared the facial signaling repertoires of two apes who exhibit dramatic differences in
627 their average group size. It is possible that variables other than group size (such as bond quality)
628 play an important role in the evolution of facial signaling repertoires. Third, we did not examine

629 the relationship between ecological variables (such as forest density, food availability, home
630 range size, etc.) and complexity in facial signaling repertoires. To fully test the *socio-ecological*
631 *complexity hypothesis*, both social and ecological variables should be considered.

632 Fourth, we did not focus on primate species outside the superfamily *Hominoidea*.
633 Additional work on other primate species (such as prosimians and monkeys) would be useful for
634 testing whether the relationship between socio-ecological complexity and communicative
635 complexity in facial signaling is widespread. For example, there are currently FACSs established
636 for multiple macaque species, including rhesus macaques (Parr et al., 2010), Barbary macaques
637 (Julle-Danière et al., 2015), crested macaques (Clark et al., 2020), and Japanese macaques
638 (Correia-Caeiro et al., 2021). Because macaques live in large multi-male, multi-female groups,
639 our *socio-ecological complexity hypothesis* predicts that these species will have large and diverse
640 facial signaling repertoires, similar to chimpanzees. However, it is plausible that limited facial
641 mobility would result in macaques having a smaller and less diverse facial signaling repertoire,
642 similar to gibbons; this would provide evidence for our *facial mobility hypothesis*. Comparisons
643 would need to be drawn between macaques, chimpanzees, and gibbons to test the relationships
644 between facial mobility, socio-ecological complexity, and facial signaling diversity/complexity.
645 Additionally, interspecific variation in facial signaling repertoires may exist due to differences in
646 social styles and ecologies among macaque species (Thierry, 2007). One recent study also found
647 that facial mobility varies among macaque species (Correia-Caeiro et al., 2021). Additional
648 comparisons would need to be made between macaque species to determine whether our *socio-*
649 *ecological complexity hypothesis* explains patterns of facial signals across all macaque species or
650 only a select few.

651 Fifth, and finally, our current study focuses on the behavior of captive primates.
652 Differences in enclosure size and visibility likely shaped the number (and kinds) of facial signals
653 we observed for both apes. The opportunity for additional social interactions were limited in part
654 by our gibbon sample, due to the fact that they are typically housed as pairs (with related
655 offspring) in isolated enclosures. While some of our gibbons had good visibility of neighboring
656 pairs (as was the case at the Gibbon Conservation Center), others were visibly isolated from
657 other pairs or housed alone (such as those housed at the Rheine Zoo). Thus, the opportunity for
658 extra-pair interactions, present in the wild, was lacking in our captive groups. For the
659 chimpanzees, the lack of wild-type fission-fusion dynamics may have constrained the contexts
660 under which they interacted. Conversely, captive environments may also facilitate a greater
661 number of social interactions which may be less frequent under wild conditions. In particular,
662 this may be the case for our troop of chimpanzees, which occupied the same enclosure and had
663 many opportunities to interact with others. The fission-fusion dynamics of wild chimpanzees
664 offers less total time together than experienced by captive groups. Additional studies with wild
665 populations of gibbons and chimpanzees are needed to verify the results of the current study.

666 The creation of FACSs for species other than humans, chimpanzees, orangutans, gibbons,
667 macaques, and marmosets would also provide opportunities to test the relationship between
668 socio-ecological complexity and communicative complexity. For example, the creation of
669 FACSs for Atelids (who exhibit fission-fusion dynamics) would provide opportunities to test the
670 relationship between social group size, facial repertoire size, and facial signaling complexity.

671 **CONCLUSION**

672 We compared the facial signaling behavior of chimpanzees (*Pan troglodytes*) and
673 gibbons (family Hylobatidae) to test two hypotheses regarding the evolution of facial signaling

674 repertoires: (1) the *facial mobility hypothesis*; and (2) the *socio-ecological complexity hypothesis*.
675 We found that chimpanzees exhibit larger and more complex facial signaling repertoires than
676 gibbons, which supports the *socio-ecological complexity hypothesis* and opposes the *facial*
677 *mobility hypothesis*. While there appear to be differences in facial mobility across apes, this does
678 not necessarily limit the number of morphologically distinct facial signals each ape can produce.
679 Having a larger and more complex facial signaling repertoire may be useful for managing
680 numerous social relationships embedded within multi-level social networks (such as those
681 observed in fission-fusion groups), whereas smaller facial signaling repertoires may be useful for
682 the management of long-term pair bonds (in the form of facial synchrony). Our results suggest
683 that multiple socio-ecological variables act on facial signals to possibly expand or contract
684 repertoire size as befitting the needs of the organisms.

685 REFERENCES

- 686 Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4),
687 227-267. <http://www.jstor.org/stable/4533591>
- 688 Andrew, R. J. (1963). The origin and evolution of the calls and facial expressions of the
689 primates. *Behaviour, Leiden*, *20*(1-2), 1-109. <https://doi.org/10.1163/156853963X00220>
- 690 Aureli, F., Schaffner, Colleen M., Boesch, C., Bearder, Simon K., Call, J., Chapman, Colin A.,
691 Connor, R., Fiore, Anthony D., Dunbar, Robin I. M., Henzi, S. P., Holekamp, K.,
692 Korstjens, Amanda H., Layton, R., Lee, P., Lehmann, J., Manson, Joseph H., Ramos-
693 Fernandez, G., Strier, Karen B., & Schaik, Carel P. v. (2008). Fission-Fusion Dynamics:
694 New Research Frameworks. *Current Anthropology*, *49*(4), 627-654.
695 <https://doi.org/10.1086/586708>

696 Barelli, C., Matsudaira, K., Wolf, T., Roos, C., Heistermann, M., Hodges, K., Ishida, T.,
697 Malaivijitnond, S., & Reichard, U. H. (2013). Extra-pair paternity confirmed in wild
698 white-handed gibbons. *Am J Primatol*, 75(12), 1185-1195.
699 <https://doi.org/10.1002/ajp.22180>

700 Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National
701 Park [<https://doi.org/10.1002/ajpa.1330780410>]. *American Journal of Physical*
702 *Anthropology*, 78(4), 547-573. <https://doi.org/https://doi.org/10.1002/ajpa.1330780410>

703 Bolker, B. (2021). *Package 'bbmle'*. Retrieved September 9 from
704 <https://github.com/bbolker/bbmle>

705 Burrows, A., Parr, L., Durham, E., Matthews, L., & Smith, T. (2014). Human Faces Are Slower
706 than Chimpanzee Faces. *PLOS ONE*, 9, e110523.
707 <https://doi.org/10.1371/journal.pone.0110523>

708 Burrows, A. M., Li, L., Waller, B. M., & Micheletta, J. (2016). Social variables exert selective
709 pressures in the evolution and form of primate mimetic musculature
710 [<https://doi.org/10.1111/joa.12440>]. *Journal of Anatomy*, 228(4), 595-607.
711 <https://doi.org/https://doi.org/10.1111/joa.12440>

712 Buttelmann, D., Call, J., & Tomasello, M. (2009). Do great apes use emotional expressions to
713 infer desires? [<https://doi.org/10.1111/j.1467-7687.2008.00802.x>]. *Developmental*
714 *Science*, 12(5), 688-698. [https://doi.org/https://doi.org/10.1111/j.1467-](https://doi.org/https://doi.org/10.1111/j.1467-7687.2008.00802.x)
715 [7687.2008.00802.x](https://doi.org/https://doi.org/10.1111/j.1467-7687.2008.00802.x)

716 Caeiro, C., Waller, B., & Burrows, A. (2013). The Cat Facial Action Coding System manual
717 (CatFACS).

718 Caeiro, C. C., Waller, B. M., Zimmermann, E., Burrows, A. M., & Davila-Ross, M. (2013).
719 OrangFACS: A Muscle-Based Facial Movement Coding System for Orangutans (*Pongo*
720 *spp.*). *International Journal of Primatology*, *34*(1), 115-129.
721 <https://doi.org/10.1007/s10764-012-9652-x>

722 Camerlink, I., Coulange, E., Farish, M., Baxter, E. M., & Turner, S. P. (2018). Facial expression
723 as a potential measure of both intent and emotion. *Scientific Reports*, *8*(1), 17602.
724 <https://doi.org/10.1038/s41598-018-35905-3>

725 Campbell, C. J., Fuentes, A., MacKinnon, K. C., Bearder, S. K., & Stumpf, R. (2010). *Primates*
726 *in Perspective* (2 ed.). Oxford University Press.

727 Christensen, R. H. B. (2019). *Package 'ordinal'*. Retrieved September 14 from
728 <https://github.com/runehaubo/ordinal>

729 Clark, P. R., Waller, B. M., Burrows, A. M., Julle-Danière, E., Agil, M., Engelhardt, A., &
730 Micheletta, J. (2020). Morphological variants of silent bared-teeth displays have different
731 social interaction outcomes in crested macaques (*Macaca nigra*)
732 [<https://doi.org/10.1002/ajpa.24129>]. *American Journal of Physical Anthropology*,
733 *173*(3), 411-422. <https://doi.org/https://doi.org/10.1002/ajpa.24129>

734 Caeiro, C., Guo, K., & Mills, D. (2017). Dogs and humans respond to emotionally competent
735 stimuli by producing different facial actions. *Scientific Reports*, *7*(15525).
736 <https://doi.org/10.1038/s41598-017-15091-4>

737 Correia-Caeiro, C., Burrows, A., Wilson, D. A., Abdelrahman, A., & Miyabe-Nishiwaki, T.
738 (2022). CalliFACS: The common marmoset Facial Action Coding System. *PLOS ONE*,
739 *17*(5), e0266442. <https://doi.org/10.1371/journal.pone.0266442>

740 Correia-Caeiro, C., Holmes, K., & Miyabe-Nishiwaki, T. (2021). Extending the MaqFACS to
741 measure facial movement in Japanese macaques (*Macaca fuscata*) reveals a wide
742 repertoire potential. *PLOS ONE*, *16*(1), e0245117.
743 <https://doi.org/10.1371/journal.pone.0245117>

744 Darwin, C. (1872). *The expression of the emotions in man and animals* [doi:10.1037/10001-
745 000]. John Murray. <https://doi.org/10.1037/10001-000>

746 Demuru, E., Ferrari, P. F., & Palagi, E. (2015). Emotionality and intentionality in bonobo playful
747 communication. *Animal Cognition*, *18*(1), 333-344. [https://doi.org/10.1007/s10071-014-](https://doi.org/10.1007/s10071-014-0804-6)
748 [0804-6](https://doi.org/10.1007/s10071-014-0804-6)

749 Dobson, S. D. (2009). Allometry of facial mobility in anthropoid primates: implications for the
750 evolution of facial expression. *Am J Phys Anthropol*, *138*(1), 70-81.
751 <https://doi.org/10.1002/ajpa.20902>

752 Ekman, P. (1970). *Universal facial expressions of emotion*

753 Ekman, P., & Friesen, W. V. (1978). *Manual for the Facial Action Code*. Palo Alto, CA:
754 Consulting Psychologist Press.

755 Ekman, P., & Rosenberg, E. L. (2005). *What the Face Reveals: Basic and Applied Studies of*
756 *Spontaneous Expression Using the Facial Action Coding System (FACS)*. New York:
757 Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780195179644.001.0001>

758 Florkiewicz, B., Skollar, G., & Reichard, U. H. (2018). Facial expressions and pair bonds in
759 hylobatids [<https://doi.org/10.1002/ajpa.23608>]. *American Journal of Physical*
760 *Anthropology*, *167*(1), 108-123. <https://doi.org/https://doi.org/10.1002/ajpa.23608>

761 Florkiewicz, B. N., & Campbell, M. W. (2021). A Comparison of Focal and Opportunistic
762 Sampling Methods when Studying Chimpanzee Facial and Gestural Communication.
763 *Folia Primatologica*, 92(3), 164-174. <https://doi.org/10.1159/000516315>

764 Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen,
765 A., & Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical
766 inference of highly parameterized complex nonlinear models. *Optimization Methods and*
767 *Software*, 27(2), 233-249. <https://doi.org/10.1080/10556788.2011.597854>

768 Freeberg, T. M. (2006). Social Complexity Can Drive Vocal Complexity: Group Size Influences
769 Vocal Information in Carolina Chickadees. *Psychological Science*, 17(7), 557-561.
770 <http://www.jstor.org/stable/40064410>

771 Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and
772 ultimate factor in communicative complexity. *Philosophical transactions of the Royal*
773 *Society of London. Series B, Biological sciences*, 367(1597), 1785-1801.
774 <https://doi.org/10.1098/rstb.2011.0213>

775 Geissmann, T. (1993). *Evolution of Communication in Gibbons (Hylobatidae)* [Ph.D.
776 Dissertation, Zürich University]. Switzerland.
777 http://www.gibbons.de/main/theses/pdf_files/1993geissmann.pdf

778 Geissmann, T., Rosenkranz-Weck, S., J.G.M. Van Der Loo, J., & Orgeldinger, M. (2020).
779 Taxon-Specific Pair Bonding in Gibbons (Hylobatidae). In *Updates on Veterinary*
780 *Anatomy and Physiology [Working Title]*. IntechOpen.
781 [https://www.intechopen.com/online-first/taxon-specific-pair-bonding-in-gibbons-](https://www.intechopen.com/online-first/taxon-specific-pair-bonding-in-gibbons-hylobatidae)
782 [hylobatidae](https://www.intechopen.com/online-first/taxon-specific-pair-bonding-in-gibbons-hylobatidae)

783 Gittins, S. P. (1980). Territorial behavior in the Agile Gibbon. *International Journal of*
784 *Primatology*, 1(4), 381-399. <https://doi.org/10.1007/BF02692281>

785 Glazko, G. V., & Nei, M. (2003). Estimation of Divergence Times for Major Lineages of
786 Primate Species. *Molecular Biology and Evolution*, 20(3), 424-434.
787 <https://doi.org/10.1093/molbev/msg050>

788 Hopkins, W. D., Tagliatela, J., & Leavens, D. A. (2007). Chimpanzees Differentially Produce
789 Novel Vocalizations to Capture the Attention of a Human. *Animal behaviour*, 73(2), 281-
790 286. <https://doi.org/10.1016/j.anbehav.2006.08.004>

791 Julle-Danière, É., Micheletta, J., Whitehouse, J., Joly, M., Gass, C., Burrows, A. M., & Waller,
792 B. M. (2015). MaqFACS (Macaque Facial Action Coding System) can be used to
793 document facial movements in Barbary macaques (*Macaca sylvanus*). *PeerJ*, 3, e1248-
794 e1248. <https://doi.org/10.7717/peerj.1248>

795 Lewinski, P., Uyl, T., & Butler, C. (2014). Automated Facial Coding: Validation of Basic
796 Emotions and FACS AUs in FaceReader. *Journal of Neuroscience, Psychology, and*
797 *Economics*, 7, 227-236. <https://doi.org/10.1037/npe0000028>

798 Liebal, K., Pika, S., & Tomasello, M. (2004). Social communication in siamangs (*Symphalangus*
799 *syndactylus*): use of gestures and facial expressions. *Primates*, 45(1), 41-57.
800 <https://doi.org/10.1007/s10329-003-0063-7>

801 Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing
802 behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, 9(1),
803 36-46. <https://doi.org/10.1007/s10071-005-0002-7>

804 Matthews, J. K. (2021). Ecological and reproductive drivers of fission-fusion dynamics in
805 chimpanzees (*Pan troglodytes schweinfurthii*) inhabiting a montane forest. *Behavioral*

806 *Ecology and Sociobiology*, v. 75(no. 1), pp. 23-23-2021 v.2075 no.2021.
807 <https://doi.org/10.1007/s00265-020-02964-4>

808 Morimoto, Y., & Fujita, K. (2012). Capuchin monkeys (*Cebus apella*) use conspecifics'
809 emotional expressions to evaluate emotional valence of objects. *Animal Cognition*, 15(3),
810 341-347. <https://doi.org/10.1007/s10071-011-0458-6>

811 Nishimura, T., Tokuda, I. T., Miyachi, S., Dunn, J. C., Herbst, C. T., Ishimura, K., Kaneko, A.,
812 Kinoshita, Y. Koda, H., Imai, H., Matsuda, T., Larsen, O. N., Jurgens, U., Hirabayashi,
813 H., Kojima, S., & Fitch, W. T. (2022). Evolutionary loss of complexity in human vocal
814 anatomy as an adaptation for speech. *Science*, 377(6607), 760-763.
815 <https://doi.org/10.1126/science.abm1574>

816 Palagi, E., Norscia, I., Pressi, S., & Cordoni, G. (2019). Facial mimicry and play: A comparative
817 study in chimpanzees and gorillas. *Emotion*, 19(4), 665-681.
818 <https://doi.org/10.1037/emo0000476>

819 Parr, L. A., Waller, B. M., Burrows, A. M., Gothard, K. M., & Vick, S. J. (2010). Brief
820 communication: MaqFACS: A muscle-based facial movement coding system for the
821 rhesus macaque. *American Journal of Physical Anthropology*, 143(4), 625-630.
822 <https://doi.org/https://doi.org/10.1002/ajpa.21401>

823 Parr, L. A., Waller, B. M., & Heintz, M. (2008). Facial expression categorization by
824 chimpanzees using standardized stimuli. *Emotion (Washington, D.C.)*, 8(2), 216-231.
825 <https://doi.org/10.1037/1528-3542.8.2.216>

826 Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial
827 expressions using muscle action. *Emotion (Washington, D.C.)*, 7(1), 172-181.
828 <https://doi.org/10.1037/1528-3542.7.1.172>

829 Pereira, A. S., Kavanagh, E., Hobaiter, C., Slocombe, K. E., & Lameira, A. R. (2020).
830 Chimpanzee lip-smacks confirm primate continuity for speech-rhythm evolution. *Biology*
831 *Letters*, 16(5), 20200232. <https://doi.org/10.1098/rsbl.2020.0232>

832 Preininger, D., Boeckle, M., Sztatecsny, M., & Hödl, W. (2013). Divergent Receiver Responses
833 to Components of Multimodal Signals in Two Foot-Flagging Frog Species. *PLOS ONE*,
834 8(1), e55367. <https://doi.org/10.1371/journal.pone.0055367>

835 Preuschoft, S. (2000). Primate Faces and Facial Expressions. *Social Research*, 67(1), 245-271.
836 <http://www.jstor.org/stable/40971384>

837 Preuschoft, S., & van Hooff, J. A. R. A. M. (1997). *The social function of "smile" and*
838 *"laughter": Variations across primate species and societies* Lawrence Erlbaum
839 Associates, Inc.

840 Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social
841 organization in mammals. *Ecology and Evolution*, 10(2), 791-807.
842 <https://doi.org/10.1002/ece3.5936>

843 Reichard, U. (1995). Extra-pair copulations in a Monogamous Gibbon (*Hylobates lar*). *Ethology*,
844 100(2), 99-112. <https://doi.org/10.1111/j.1439-0310.1995.tb00319.x>

845 Roberts, A. I., & Roberts, S. G. B. (2019). Persistence in gestural communication predicts
846 sociality in wild chimpanzees. *Animal Cognition*, 22(5), 605-618.
847 <https://doi.org/10.1007/s10071-018-1219-6>

848 Ryne, A. P. (1996). Pair Bonds in Monogamous Apes: A Comparison of the Siamang *Hylobates*
849 *syndactylus* and the White-Handed Gibbon *Hylobates lar*. *Behaviour*, 133(5/6), 321-356.
850 <http://www.jstor.org/stable/4535362>

851 Ryne, P. (1994). Dynamic Pair Bonds in Hylobatids: Implications regarding Monogamous Social
852 Systems. *Behaviour*, 128(1/2), 65-101. <http://www.jstor.org/stable/4535165>

853 Scheider, L., Liebal, K., Oña, L., Burrows, A., & Waller, B. (2014). A comparison of facial
854 expression properties in five hylobatid species. *American Journal of Primatology*, 76(7),
855 618-628. <https://doi.org/https://doi.org/10.1002/ajp.22255>

856 Scheider, L., Waller, B. M., Oña, L., Burrows, A. M., & Liebal, K. (2016). Social Use of Facial
857 Expressions in Hylobatids. *PLOS ONE*, 11(3), e0151733.
858 <https://doi.org/10.1371/journal.pone.0151733>

859 Silk, J. (2002). Grunts, girneys, and good intentions: The origins of strategic commitment in
860 nonhuman primates. *Commitment: Evolutionary Perspectives*, 138-157.

861 Smith, M. J., & Harper, D. G. C. (1995). Animal Signals: Models and Terminology. *Journal of*
862 *Theoretical Biology*, 177(3), 305-311.
863 <https://doi.org/https://doi.org/10.1006/jtbi.1995.0248>

864 Southwick, C. H. (1985). THE LESSER APES: EVOLUTIONARY AND BEHAVIOURAL
865 BIOLOGY. *Evolution*, 39(6), 1399-1400. [https://doi.org/https://doi.org/10.1111/j.1558-](https://doi.org/https://doi.org/10.1111/j.1558-5646.1985.tb05708.x)
866 [5646.1985.tb05708.x](https://doi.org/https://doi.org/10.1111/j.1558-5646.1985.tb05708.x)

867 Sueur, C., Deneubourg, J.-L., Petit, O., & Couzin, I. D. (2011). Group size, grooming and fission
868 in primates: A modeling approach based on group structure. *Journal of Theoretical*
869 *Biology*, 273(1), 156-166. <https://doi.org/https://doi.org/10.1016/j.jtbi.2010.12.035>

870 Terleph, T. A., Malaivijitnond, S., & Reichard, U. H. (2018). An analysis of white-handed
871 gibbon male song reveals speech-like phrases. *American Journal of Physical*
872 *Anthropology*, 166(3), 649-660. <https://doi.org/10.1002/ajpa.23451>

873 Thierry, B. (2007). Unity in diversity: Lessons from macaque societies
874 [<https://doi.org/10.1002/evan.20147>]. *Evolutionary Anthropology: Issues, News, and*
875 *Reviews*, 16(6), 224-238. <https://doi.org/https://doi.org/10.1002/evan.20147>

876 Thierry, B. (2013). Identifying constraints in the evolution of primate societies. *Philosophical*
877 *transactions of the Royal Society of London. Series B, Biological sciences*, 368(1618),
878 20120342. <https://doi.org/10.1098/rstb.2012.0342>

879 Van Hooff, J. A. R. A. M. (1967). *The Facial Displays of the Catarrhine Monkeys and Apes*

880 Vick, S.-J., Waller, B. M., Parr, L. A., Smith Pasqualini, M. C., & Bard, K. A. (2007). A Cross-
881 species Comparison of Facial Morphology and Movement in Humans and Chimpanzees
882 Using the Facial Action Coding System (FACS). *Journal of nonverbal behavior*, 31(1),
883 1-20. <https://doi.org/10.1007/s10919-006-0017-z>

884 Waller, B. M., & Dunbar, R. I. M. (2005). Differential Behavioural Effects of Silent Bared Teeth
885 Display and Relaxed Open Mouth Display in Chimpanzees (Pan troglodytes). *Ethology*,
886 111(2), 129-142. <https://doi.org/https://doi.org/10.1111/j.1439-0310.2004.01045.x>

887 Waller, B. M., Julle-Daniere, E., & Micheletta, J. (2020). Measuring the evolution of facial
888 ‘expression’ using multi-species FACS. *Neuroscience & Biobehavioral Reviews*, 113, 1-
889 11. <https://doi.org/https://doi.org/10.1016/j.neubiorev.2020.02.031>

890 Waller, B. M., Kavanagh, E., Micheletta, J., Clark, P. R., & Whitehouse, J. (2022). The face is
891 central to primate multicomponent signals. *International Journal of Primatology*.
892 <https://doi.org/10.1007/s10764-021-00260-0>

893 Waller, B. M., Lembeck, M., Kuchenbuch, P., Burrows, A. M., & Liebal, K. (2012).
894 GibbonFACS: A Muscle-Based Facial Movement Coding System for Hylobatids.

895 *International Journal of Primatology*, 33(4), 809-821. <https://doi.org/10.1007/s10764->
896 [012-9611-6](https://doi.org/10.1007/s10764-012-9611-6)

897 Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski,
898 J. (2013). Paedomorphic Facial Expressions Give Dogs a Selective Advantage. *PLOS*
899 *ONE*, 8(12), e82686. <https://doi.org/10.1371/journal.pone.0082686>

900 Waller, B. M., Warmelink, L., Liebal, K., Micheletta, J., & Slocombe, K. E. (2013).
901 Pseudoreplication: a widespread problem in primate communication research. *Animal*
902 *behaviour*, 86(2), 483-488. <https://doi.org/https://doi.org/10.1016/j.anbehav.2013.05.038>

903 Waller, B. M., Whitehouse, J., & Micheletta, J. (2016). Macaques can predict social outcomes
904 from facial expressions. *Animal Cognition*, 19(5), 1031-1036.
905 <https://doi.org/10.1007/s10071-016-0992-3>

906 Wathan, J., Burrows, A. M., Waller, B. M., & McComb, K. (2015). EquiFACS: The Equine
907 Facial Action Coding System. *PLOS ONE*, 10(8), e0131738.
908 <https://doi.org/10.1371/journal.pone.0131738>

909 Whiten, A. B., Richard W. (1997). *Machiavellian intelligence II: Extensions and evaluations*
910 [doi:10.1017/CBO9780511525636]. Cambridge University Press.
911 <https://doi.org/10.1017/CBO9780511525636>

912