Received: 21 April 2019 | Revised: 27 January 2020 | Accepted: 10 February 2020

DOI: 10.1002/ajpa.24031

RESEARCH ARTICLE

American Journal of PHYSICAL ANTHROPOLOGY WILEY

The structural and motivational role of the unique lip-flip movement in the gelada (*Theropithecus gelada*) facial display repertoire

Stefanie P. Lazow[1,2] | Thore J. Bergman[3]

[1]Department of Anthropology, Dartmouth College, Hanover, New Hampshire

[2]Department of Surgery, Beth Israel Deaconess Medical Center, Harvard Medical School, Boston, Massachusetts

[3]Department of Psychology, University of Michigan, Ann Arbor, Michigan

Correspondence
Stefanie P. Lazow, 110 Francis St., Suite 9B, Department of Surgery, Beth Israel Deaconess Medical Center, Boston, MA 02215.
Email: slazow@bidmc.harvard.edu

Funding information
Claire Garber Goodman Fund, Dartmouth College; National Geographic Society; National Science Foundation, Grant/Award Numbers: NSF-1340911, BCS-0715179, BCS-0962118, IOS-1255974; The Leaky Foundation; University of Michigan

Abstract

Objectives: Human language represents an extreme form of communicative complexity. Primate facial display complexity, which depends upon facial mobility, can be used as a model for the study of the evolution of communicative complexity. The gelada (*Theropithecus gelada*) is the only primate that can produce a lip-flip eversion. This study investigates the role of the lip-flip relative to the bared-teeth display to understand its role in generating communicative complexity.

Materials and methods: We reviewed videos of gelada social interactions. We utilized the facial action coding system (FACS) to define structural component action units (AUs) of each display. We inferred display motivation from the behaviors of the display sender.

Results: The lip-flip was used only in combination with the essential AUs of the bared-teeth display, serving as an optional structural element added to produce a structural variant. Both the bared-teeth display with and without a lip-flip occurred most frequently with nonaggressive, submissive behaviors. The lip-flip was more frequently preceded by approach than the bared-teeth display, especially in males. The lip-flip was also present in the majority of structurally blended facial displays though the motivation of the non-lip-flip parent display often dominated.

Discussion: The lip-flip may potentially function as an indicator of benign intent after an approach or as an intensifying component of nonaggressive intent. Adaptations to increase facial mobility in geladas via facilitating the lip-flip may promote increased communicative complexity through increased conspicuousness and motivational signaling specification or intensification.

KEYWORDS

bared-teeth display, facial display, facial expression, facial mobility, gelada

1 | INTRODUCTION

Human language represents an extreme form of communicative complexity. In an attempt to understand how this degree of complexity arose, prior researchers have focused on better understanding vocalizations in birds (e.g., Freeberg, 2006; Kroodsma, 1977) and primates (e.g., Braune, Schmidt, & Zimmerman, 2008; Gamba, Friard, & Giacoma, 2012; Gustison & Bergman, 2016; Kean et al., 2017; McComb & Semple, 2005; Zimmerman, 2017). However, the gestural theory of language evolution suggests that human language originally developed from gestural or manual communication, progressing first to facial displays and then finally to vocal communication

(Corballis, 2010; Gentilucci & Corballis, 2006). In addition, regardless of its role in facial displays, facial mobility is directly tied to speech production (Ghazanfar & Takahashi, 2014). Despite this potential important role of facial displays and facial mobility in the evolution of human language, much less is known about the evolution of complexity within primate facial communication systems.

Primates use facial displays, often in conjunction with vocalizations, to facilitate close-range social interactions by providing information to the receiver about the immediate future behavior of the signaler (Maynard Smith & Harper, 2003; Parr, Waller, & Micheletta, 2015; Waller & Michelatta, 2013). Facial displays are compound expressions, composed of a combination of independent facial muscle movements. Investigating the origins of increased facial mobility is therefore integral to understanding the evolution of increased complexity of auditory and visual communication involving movements of the face, including language.

In contrast to the high degree of variation in the size of primate vocal call repertoires (McComb & Semple, 2005; Zimmerman, 2017), there appears to be minimal diversity in primate facial display repertoire size, or the number of discrete facial displays that a primate species can produce (Scheider, Liebal, Ona, Burrows, & Waller, 2014; van Hooff, 1967), though this may be an artifact of relatively limited research efforts. Similarly, facial musculature anatomy is also remarkably consistent across different primate species (Burrows, 2008).

However, focusing on limited display repertoire size obscures important variation within repertoires in two ways. First, structural blending of discrete displays and the use of multimodal displays can increase communicative complexity without truly increasing repertoire size. Blended facial displays show structural features that are common to at least two discrete, peak-intensity display types (Parr, Cohen, & de Waal, 2005). In an early study of primate communication, Marler (1965) declared that the intergrading of facial signals within primate repertoires was so widespread "as to be virtually the rule rather than the exception." Moreover, primates often utilize multimodal displays (combined displays from different sensory modalities) to increase communicative complexity via several mechanisms including enhancement, antagonism, or modulation of signal meaning, versus possible emergence of a new signal meaning (Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013; Partan & Marler, 1999).

Second, there is considerable variation in primate facial mobility with increased group size, as a proxy for social complexity, predicting increased facial mobility (Dobson, 2009a; Dobson, 2009b). This variation in facial mobility has the potential to increase communicative complexity within facial display repertoires by allowing for potential modification or amplification of already existing display types. Whether this produces graded versions of the same display without impacting repertoire size, representing concealed variation within the repertoire, or fundamentally creates new displays to increase repertoire size is a matter of unresolved controversy; nonetheless, either mechanism results in increased communicative complexity.

One of the best-known examples of an evolutionary increase in facial mobility is the development of the unique lip-flip movement of the gelada (*Theropithecus gelada*), which other primates do not produce. During the lip-flip, the upper lip is pulled upwards and everted (Figure 1). Unlike other primates, geladas have a unique muscular apparatus involving the upper lip to promote this eversion. The fibers of the levator labii superiosis and zygomaticus muscles, which run longitudinally along the muzzle, are virtually fused together and continue to the free edge of the upper lip, obscuring the orbicularis oris (Hill, 1969). These fused fibers then function together to form a sling that facilitates upper lip eversion (Hill, 1969).

Given the previously demonstrated relationship between facial mobility and social complexity (Dobson, 2009b), the gelada further represents an ideal model because geladas live in large, multilevel social groups (Kawai, Ohsawa, Mori, & Dunbar, 1983; Snyder-Mackler, Beehner, & Bergman, 2012). Therefore, increased communicative complexity capacity could be adaptive in this setting (Freeberg, Dunbar, & Ord, 2012). However, the gelada facial display repertoire has not been systematically studied, and there has been persistent controversy within the popular press and scientific community regarding the role of the lip-flip.

Within the popular press, the lip-flip is consistently considered aggressive despite prior research suggesting a relationship between the lip-flip and the nonaggressive bared-teeth display. Previous researchers have provided conflicting descriptions of the structural role and motivational basis of the lip-flip (Alvarez & Consul, 1978; Bramblett, 1970; Dunbar & Dunbar, 1975; Fedigan, 1972; Kawai, 1979; Mori, 1979a; Mori, 1979b; van Hooff, 1967). In 1967, van Hooff first described the lip-flip as a display element used in combination with both the silent bared-teeth display and the staring bared-teeth scream face, each representing different motivational tendencies (van Hooff, 1967). Alvarez and Consul (1978), Mori (1979a, 1979b), and Kawai (1979) proposed an affiliative motivational basis. In contrast, Bramblett (1970) and Fedigan (1972) later described an aggressive "lip-roll" display in captive geladas. Dunbar and Dunbar (1975) instead hypothesized that the lip-flip reflects underlying "uncertainty/crisis" given frequent co-occurrence with self-directed behaviors such as yawning.

Given the inconsistencies within the prior literature, this study will first systematically analyze both the structural and motivational roles of the lip-flip movement to document the communicative value of this unique facial movement. Second, lip-flip integration into blended displays will also be analyzed as another potential mechanism for increasing communicative complexity.

2 | MATERIALS AND METHODS

2.1 | Video collection

This study had IACUC approval from Dartmouth College; all work was in accordance with the U.S. National Research Council's Guide for the Care and Use of Laboratory Animals, the U.S. Public Health Service's Policy on Humane Care and Use of Laboratory Animals, and Guide for the Care and Use of Laboratory Animals. S. Dobson collected video footage of social interactions among 200–300 wild geladas organized in approximately 20 reproductive units during fieldwork conducted

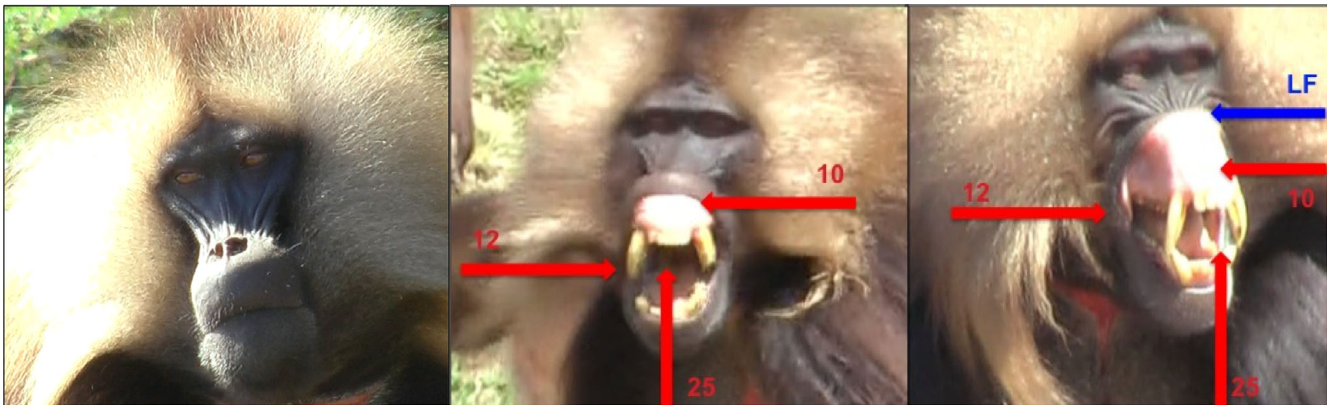

FIGURE 1 The gelada rest face is presented on the left. The bared-teeth display, defined by the inclusion of essential action units (AUs) 10 (upper lip raiser) + 12 (lip corner puller) + 25 (lips part) is presented in the center. The "lip-flip" display (right) included the same essential AUs (10 + 12 + 25) in addition to the lip-flip (LF) movement (blue). Additional optional AUs (16, lip depress, and 27, mouth stretch) are present but not labeled in both displays depicted here

over a five-week period in 2008 in the Michiby and Chilquanit areas of Simien Mountains National Park, Ethiopia. The observer recorded three to four reproductive units per day, observing the same reproductive unit on average once every five to six days, to minimize the risk of pseudoreplication bias from sampling the same individual multiple times (Waller, Warmelink, Liebal, Michelatta, & Sclocombe, 2013).

The observer collected digital high-definition video recordings ad-libitum during peak hours of social activity, usually between 08:00 and 12:00, using a Panasonic HDC-SD5 high definition camcorder. In total, there was 17 hr of video separated into 104 clips. The first author (SL) analyzed the videos in 2011, thereby avoiding potential problems with inter-observer reliability. The identity of individual monkeys could not be determined from the video analysis due to the narrow frame of reference. However, given the large number of animals and the rotation system between different reproductive units during video collection, the likelihood of sampling the same individual multiple times was low, though this possibility cannot be fully excluded.

2.2 | Display structural analysis

We defined facial displays as a single facial movement (action unit, or AU), a combination of facial movements occurring discretely in time, or a combination of facial movements in continuous sequence. We defined a continuous sequence as a sequence of AUs occurring without a pause or return to the baseline resting face. Facial movements involved in food chewing, yawning, and jaw-fencing (a combat posture that involves attacking with a wide-open mouth) were excluded because these behaviors are not definitively considered communicative to promote a more conservative motivational analysis. For each facial display, we recorded the sex of the displayer. We only analyzed adult displays due to difficulty discerning sex in juveniles.

First author SL, who is certified in the Facial Action Coding System (FACS; Ekman, Friesen, & Hager, 2002), then applied the human FACS to each facial display. FACS certification is achieved after passing the FACS Final Test, which is the standard measure for proficiency. FACS assigns each facial movement a unique AU (see Table Table S1 for a list of all AUs); the component AUs of each display were coded. We modified human FACS based upon prior research using FACS in nonhuman anthropoids (Dobson, 2006; Dobson, 2009a) as well as a review of modifications utilized in MaqFACS (Parr, Waller, Burrows, Gothard, & Vick, 2010) and ChimpFACS (Parr, Waller, Vick, & Bard, 2007). OrangFACS and GibbonFACS also provide modifications for use in other taxa (Caeiro, Waller, Zimmerman, Burrows, & Davila-Ross, 2013; Waller, Lembeck, Kuchenbuch, Burrows, & Liebal, 2012).

Table 1 provides detailed modifications made to human FACS for this application (Dobson, 2009a). For example, we coded AU 1 and AU 2 in combination as AU 1 + 2 because nonhuman anthropoids cannot independently move the medial and lateral portions of the eyebrow. We recorded the presence of a lip-flip eversion movement in addition to AU 10 (upper lip raiser), but we did not assign a separate AU for this eversion movement. We excluded certain upper face AUs (5–7) from analysis because the video was often not zoomed in to reliably discern these AUs. We excluded AUs describing head and eye movements.

The first author (SL) randomly selected a subset of facial displays (10% of all coded displays, $n = 97$) for blinded repeat AU coding to facilitate reliability testing. We calculated intra-observer reliability in two ways, which is reported in Table Table S1. We calculated an absolute intra-observer agreement based upon percentage of concordant coding per AU. Next, we calculated a chance-corrected Cohen's Kappa agreement score, which is reported with 95% confidence intervals per AU (Viera & Garrett, 2005; Table Table S1). Absolute intra-observer agreement for the lip-flip movement was 100% and Cohen's Kappa was 1. Cohen's Kappa agreement was slight for AU 26 ($\kappa = 0.18$), moderate for AU 16 ($\kappa = 0.55$), and substantial to almost perfect for AU 1 + 2 ($\kappa = 0.91$), AU 4 ($\kappa = 0.69$), AU 10 ($\kappa = 0.96$), AU 12 ($\kappa = 0.96$), AU 17 ($\kappa = 0.70$), AU 19 ($\kappa = 0.67$), AU 25 ($\kappa = 0.95$), and AU 27 ($\kappa = 0.77$). We excluded AU 26 (jaw drop) from subsequent analysis due to only slight agreement. We still included AU 16 (lower

TABLE 1 Most-useful FACS coding criteria for nonhuman anthropoids[a,b]

Action unit	Appearance change
1 + 2	Pulls the medial and lateral parts of the brow upwards
4	Lowers the entire brow region by pulling the anterior part of the scalp downward
9	Pulls the skin above the nose upward toward the orbits causing horizontal wrinkles across the infraorbital region
10	Raises the upper lip causing the lips to part
12	Pulls the corners of the lips backward
13	Pulls the corners of the lips upward sharply without pulling them backward
14	Tightens the corners of the lips causing an oblique wrinkle at corner
15	Pulls the corners of the lips downward
16	Pulls the lower lip down causing the lips to part
17	Protrudes the lips
18	Pulls the lip corners medially causing the mouth opening to shrink
22	Parts and everts the lips causing them to turn outward
23	Tightens the lips causing vertical wrinkles above and below the lips
24	Presses the lips together causing bulging above and below the lips
28	Pulls the lips inward causing the skin to stretch over the teeth

[a]Table directly reproduced from Dobson (2009a).
[b]Based on a subjective assessment of the similarity of nonhuman anthropoid muscle actions to the criteria defined by the human Facial Action Coding System, or FACS (Ekman et al., 2002).

lip depress) despite having moderate agreement because of minimal impact on other analyses. Cohen's Kappa could not be calculated for rare AUs (AU 9, AU 13, AU 14, AU 15, AU 18, AU 20, AU 22, AU 23, AU 24, AU 28).

Several prior researchers (Alvarez & Consul, 1978; Dunbar & Dunbar, 1975; van Hooff, 1967) have described the lip-flip movement as an expression element that is part of the bared-teeth display (BT; see Introduction). We therefore initially investigated the relationship between the structure of the BT display and the lip-flip. Based upon descriptions of the structure of the BT display in other primates (including chimpanzees, macaques, and mandrills), we defined the gelada BT display as AU 10 (upper lip raiser), AU 12 (lip corner puller), and AU 25 (lips part) (Figure 1; Bout & Thierry, 2005; Parr et al., 2007; Parr & Waller, 2006; Thierry, Demaria, Preuschoft, & Desportes, 1989).

2.3 | Display behavioral analysis

For each facial display, we coded and categorized behaviors performed by the individual producing the facial movements, that is, the "sender" of the signal, based upon Dunbar and Dunbar (1975). We defined behaviors occurring within 5 s of facial display onset as occurring before the display, behaviors occurring between onset and offset of the facial display as occurring during the display, and behaviors occurring within 5 s after the display offset as occurring after the display. We defined display onset as the first discernable facial movement away from the rest (neutral) position, and offset was defined as the full return of all facial features to the rest position.

Based upon Dunbar and Dunbar's (1975) classification, we categorized sender behaviors into aggressive, nonaggressive, and neutral behaviors (Table S2). We further classified nonaggressive behaviors as either affinitive or submissive (Dunbar & Dunbar, 1975). We also included two additional behaviors that we observed but were not in the original ethogram including: grooming presentation (nonaggressive), referring to receiving grooming from another individual, and standing up (neutral), referring to standing on the hindlimbs only. We then used sender behaviors associated with facial displays to infer the motivational state of the sender as aggressive, nonaggressive, or mixed. We classified displays without associated social behaviors and displays occurring with the neutral standing up behavior in a "no sender behavior" category. We categorized sender behaviors separately before, during, and after the display to infer the motivation of the individual occurring during those time intervals. We compared BT displays with and without a lip-flip in two ways. First, we compared the frequency of each display type occurring with sender behaviors reflecting each inferred motivational state at each time point. Second, to provide contextual analysis, we compared the frequency of all nonaggressive or aggressive displays collected opportunistically that represented either type of display. However, this type of analysis was limited due to the likely inability of the opportunistic sampling technique to capture accurate baseline behavioral rates. Narrow video focus prevented collection of data on sender identity or receiver behaviors.

2.4 | Display blending

We investigated the blending of three well-described gelada displays including the BT display ± the lip-flip (coded as BTLF when present), the lip-smack (LS), and the eyebrow raise (EB). We defined these displays by the presence of essential AUs based upon previous literature. The LS display was defined as AU 17 (chin raiser), AU 25 (lips part), and a jaw raise movement (JR; not defined as an AU in human FACS) with optional AU 19 (tongue protrusion). The EB display was defined as AU 1 + 2 (brow raiser). We defined a structural blend as a display containing all the essential AUs from more than one parent display, with any combination of nonessential AUs. We excluded displays that had uncodable upper face movements from blending analysis because the essential AU 1 + 2 in the EB display could not be coded in those cases. For displays that were structurally blended, we then performed an additional analysis to determine if associated sender behaviors reflected blended or unblended parent display motivations. We then pooled sender behaviors occurring before, during, and/or after the display for blending analysis.

TABLE 2 Comparison of observed action units (AU) in bared-teeth displays without a lip-flip (BT) versus bared-teeth displays with a lip-flip (BTLF)

AU	AU description	% BT displays with AU (*n* = 106)	% BTLF displays with AU (*n* = 260)	X^{2*}	*p* value*
1 + 2	Brow raiser[a]	29 (31.2%)	53 (25.5%)	1.05	.31
4	Brow lowerer[b]	41 (44.1%)	55 (33.3%)	2.94	.09
9	Nose wrinkle	0 (0.0%)	1 (0.4%)	n/a	>.99
10	Upper lip raiser	106 (100.0%)	260 (100.0%)	–	–
12	Lip corner puller	106 (100.0%)	260 (100.0%)	–	–
13	Sharp lip puller	0 (0.0%)	0 (0.0%)	–	–
14	Dimpler	0 (0.0%)	0 (0.0%)	–	–
15	Lip corner depressor	0 (0.0%)	0 (0.0%)	–	–
16	Lower lip depress	94 (88.7%)	249 (95.8%)	6.43	.01**
17	Chin raiser	37 (34.9)%	82 (31.5%)	0.39	.53
18	Lip pucker	0 (0.0%)	0 (0.0%)	–	–
19	Tongue show	26 (24.5%)	53 (20.4%)	0.76	.38
20	Lip stretch	0 (0.0%)	0 (0.0%)	–	–
22	Lip funneler	0 (0.0%)	0 (0.0%)	–	–
23	Lip tightener	0 (0.0%)	0 (0.0%)	–	–
24	Lip presser	3 (2.8%)	4 (1.5%)	n/a	.42
25	Lips part	106 (100.0%)	260 (100.0%)	–	–
27	Mouth stretch	56 (52.8%)	175 (67.3%)	6.78	.009**
28	Lips suck	0 (0.0%)	0 (0.0%)	–	–

[a]BT *n* = 98, BTLF *n* = 208 due to exclusion of uncodable displays for AU 1 + 2.
[b]BT *n* = 93, BTLF *n* = 165 due to exclusion of uncodable displays for AU4.
*Chi-square value is not available if fisher's exact test was performed. Degrees of freedom = 1. *p* values refer to chi-square or fisher's exact analysis results, as appropriate.
***p* values are significant at ≤.05 level.

2.5 | Display analysis and statistics

We performed structural and behavioral analyses only within the pool of displays that had codable criteria for that specific test. Thus, percentages, unless otherwise noted, refer only to the group of displays with codable criteria. We performed statistical analysis using SPSS (version 22, Armonk, NY). Univariate analysis included use of Chi-square analysis and Fisher's exact test, as appropriate, to compare frequency of BT displays containing lip-flip movements in males versus females, differences in AU frequency between BT versus BTLF displays (Table 2), and differences in frequency of aggressive sender behaviors occurring during the BT/BTLF display and the EB display. In Table 3, we performed Chi-square analysis to compare the differences in frequency of BT and BTLF displays occurring with sender behaviors reflecting different inferred motivational states (nonaggressive, aggressive, mixed, or no associated behavior) at different time-points. Next, we performed post hoc pairwise comparison using Bonferroni-corrected *z* tests (Waller, Whitehouse, & Micheletta, 2016) to compare frequencies of BT and BTLF displays occurring with each specific inferred motivational state at each time-point. All *p* values are two-sided with statistical significance reported at the 0.05 alpha level.

3 | RESULTS

3.1 | Structural analysis

A total of 966 adult facial displays were initially coded. Males produced 803 (83.1%) displays and females produced 153 (15.8%), while individuals of indeterminate sex produced 10 (1.0%). A lip-flip movement was present in 362 displays (37.5%). We excluded displays that occurred during yawning (*n* = 103) and jaw-fencing (*n* = 23) from subsequent analyses; 76.7% of yawns (*n* = 79) and 100% of jaw-fencing bouts involved the lip-flip. The remaining 260 lip-flip displays accounted for 31% of all presumably communicative facial displays (*n* = 840). Males produced 231 (88.9%) of the 260 lip-flip-containing displays, while females produced 26 (10.0%) and individuals of indeterminate sex produced three (1.1%).

First, we investigated the relationship between the structure of the BT display and the lip-flip. The essential BT-defining AUs (AU 10 + 12 + 25) co-occurred in 366 displays (43.6%), which we defined as BT displays. Of the 366 BT displays, 71.0% included a lip-flip. Of the 276 male BT displays, 231 (83.7%) contained a lip-flip whereas only 26 out of 85 (30.6%) female BT displays contained a lip-flip, reflecting a significant difference on Chi-square analysis (X^2[1, *N* = 366] = 89.39,

TABLE 3 Motivational basis of bared-teeth displays without a lip-flip (BT) versus bared-teeth displays with a lip-flip (BTLF)

	BT displays* [*N* (%)]	BTLF displays* [*N* (%)]	X^2**	*p* value**
Motivational basis before[a]			4.53	0.21
Nonaggressive	31 (45.6%) a	82 (47.1%) a		
Aggressive	18 (26.5%) a	29 (16.7%) a		
Mixed (nonaggressive and aggressive)	4 (5.9%) a	7 (4.0%) a		
No sender behavior	15 (22.1%) a	56 (32.2%) a		
Motivational basis during[b]			7.73	0.05**
Nonaggressive	62 (59.0%) a	138 (54.1%) a		
Aggressive	18 (17.1%) a	28 (11.0%) a		
Mixed (nonaggressive and aggressive)	8 (7.6%) a	15 (5.9%) a		
No sender behavior	17 (16.2%) a	74 (29.0%) b		
Motivational basis after[c]			10.86	0.01*
Nonaggressive	65 (70.7%) a	144 (63.7%) a		
Aggressive	18 (19.6%) a	29 (12.8%) a		
Mixed (nonaggressive and aggressive)	4 (4.3%) a	9 (4.0%) a		
No sender behavior	5 (5.4%) a	44 (19.5%) b		

[a] *N* = 242 codable displays for motivational basis before the display.
[b] *N* = 360 codable displays for motivational basis during the display.
[c] *N* = 318 codable displays for motivational basis after the display.
*Letters represent the results of the post hoc pairwise comparison using Bonferroni-corrected *z* tests. A difference in letters indicates a significant pairwise difference between BT and BTLF displays in that specific motivational basis ($p \leq .05$).
**X^2 and *p* values refer to chi-square results performed per time-point. Degrees of freedom = 3.

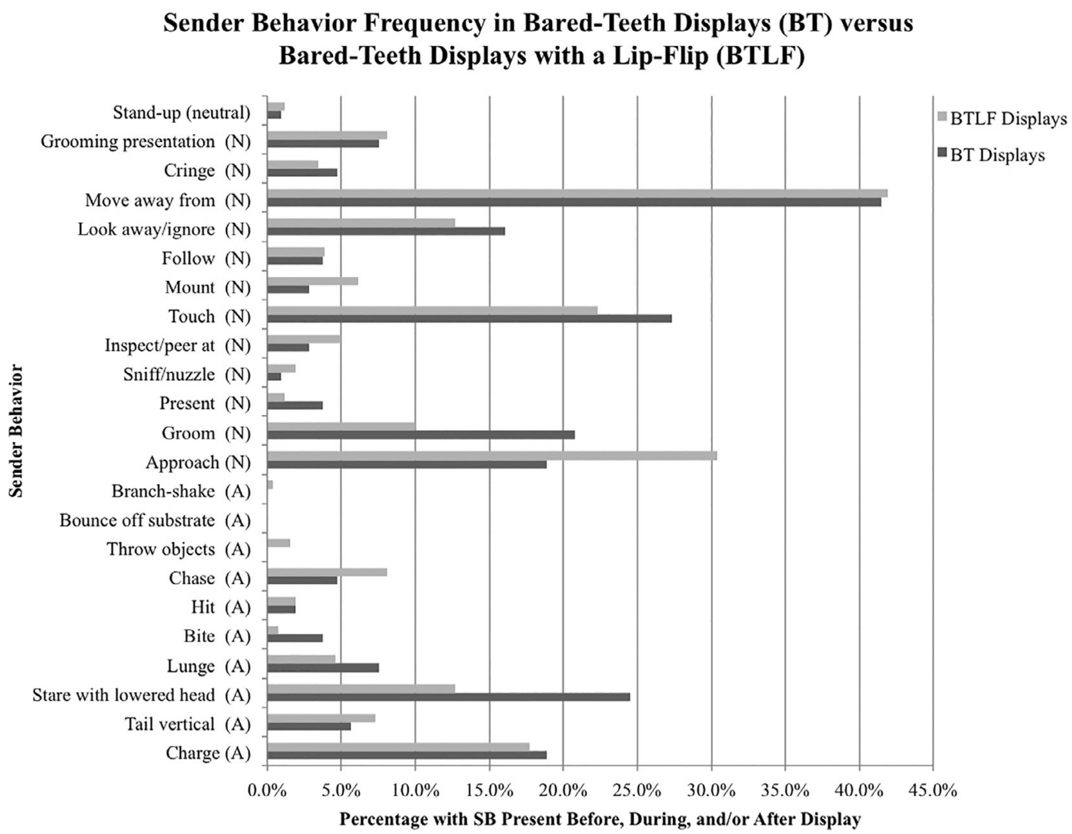

FIGURE 2 This graph compares the percentage of sender behaviors (SB) occurring at pooled frequencies before, during, and/or after bared-teeth displays without a lip-flip (BT) versus bared-teeth displays with a lip-flip (BTLF). SB are classified as aggressive (A), nonaggressive (NA), or neutral

$p < .001$). While not all BT displays included lip-flips, all displays containing a lip-flip included all three AUs that define the BT display (Figure 1).

TABLE 4 Frequency of structurally blended displays

Display combination	Action unit (AU) definition	*N* (%[a])
BT + LS	10 + 12 + 17 + 25 + JR; no 1 + 2 + LF	26 (3.4%)
BT + EB	1 + 2 + 10 + 12 + 25; no 17 + LF	25 (3.3%)
BTLF + LS	17 + JR + LF; no 1 + 2	52 (6.9%)
BTLF + EB	1 + 2 + LF; no 17	41 (5.4%)
LS + EB	1 + 2 + 17 + 25 + JR; no 10 + 12 + LF	32 (4.2%)
BT + LS + EB	1 + 2 + 10 + 12 + 17 + 25 + JR; no LF	4 (0.5%)
BTLF + LS + EB	1 + 2 + 10 + 12 + 17 + 25 + JR + LF	11 (1.5%)
Total blended displays		191 (25.2%)

Abbreviations: BT, bared-teeth display without a lip-flip; LS, lip-smack display; EB, eyebrow raise display; BTLF, bared-teeth display with a lip-flip; LF, lip-flip; JR, jaw raise.
[a]Percentage out of 759 displays available for blending analysis.

When comparing nonessential AUs between BT (n = 106) and BTLF displays (n = 260), the majority had no statistically significant differences in frequency (Table 2). The nonessential AUs with significant differences in frequency between BT and BTLF displays were AU 16 (88.7% vs. 95.8%; $X^2[1, N = 366] = 6.43$, $p = .01$) and AU 27 (52.8% vs. 67.3%; $X^2[1, N = 366] = 6.78$, $p = .009$).

3.2 | Behavioral analysis

Inferred motivational states of displays and univariate statistical analysis results are summarized in Table 3. Both BT and BTLF displays occurred more frequently with nonaggressive sender behaviors than aggressive sender behaviors over all time periods. BT displays consistently occurred more frequently with aggressive sender behaviors at all time points compared to BTLF displays (23.7% vs. 17.9%). Chi-square analysis found a statistically significant difference between the frequency of BT and BTLF displays occurring with different inferred motivational states based upon sender behaviors occurring during ($X^2[3, N = 360] = 7.73$, $p = .05$) and after the displays ($X^2[3, N = 318] = 10.86$, $p = .01$), though not before ($X^2[3, N = 242] = 4.53$, $p = .21$). Post hoc pairwise comparison showed that BTLF displays occurred significantly more frequently than BT displays with no associated sender behaviors both during (29.0% vs. 16.2%) and after

FIGURE 3 These images depict structural blending within the gelada facial display repertoire: (a) unblended bared-teeth display with lip-flip (BTLF) (top left), (b) unblended eyebrow raise display (EB) (top center), (c) BTLF + EB structural blend (top right), (d) unblended BTLF (bottom left), (e) unblended lip-smack display (LS) (bottom center), (f) BTLF + LS structural blend (bottom right)

TABLE 5 The motivational bases of unblended versus blended gelada facial displays

	N (%[a]) unblended motivation	*N* (%[a]) blended motivation
Unblended BT	18 (72.0%)	7 (28.0%)
Unblended BTLF	40 (60.6%)	26 (39.4%)
Unblended LS	67 (73.6%)	24 (26.4%)
Unblended EB	143 (56.5%)	110 (43.5%)
BT + LS blend	16 (64.0%)	9 (36.0%)
BT + EB blend	18 (75.0%)	6 (25.0%)
BTLF + LS blend	31 (66.0%)	16 (34.0%)
BTLF + EB blend	18 (51.4%)	17 (48.6%)
LS + EB blend	14 (46.7%)	16 (53.3%)
BT + LS + EB blend	0 (0.0%)	4 (100.0%)
BTLF + LS + EB blend	6 (60.0%)	4 (40.0%)

Abbreviations: BT, bared-teeth display without a lip-flip; BTLF, bared-teeth display with a lip-flip; LS, lip-smack display; EB, eyebrow raise display.
[a]Percentages are calculated by row from the total number of displays included in this sub-analysis of most common sender behaviors within the submissive, affinitive, and aggressive categories.

(19.5% vs. 5.4%) displays. There were no other significant differences in BT and BTLF frequency occurring with each inferred motivational state.

Examination of all displays with aggressive sender behaviors occurring during the display (n = 256) revealed that 18 of those displays were BT displays (7.0%) and 28 were BTLF displays (10.9%). Analysis of all displays with nonaggressive sender behaviors occurring during the display (n = 348) revealed that 62 of those displays were BT displays (17.8%) and 138 were BTLF displays (39.7%).

Compared to the EB display, which is an established aggressive display, both BT and BTLF displays occurred with significantly fewer aggressive behaviors during the display on Chi-square analysis (EB: 65.9% vs. BT: 17.1%, $X^2[3, N = 372] = 112.57$, $p < .001$; EB: 65.9% vs. BTLF: 11.0%, $X^2[3, N = 522] = 206.24$, $p < 0.001$).

The frequencies of specific sender behaviors occurring at pooled frequencies before, during, and/or after BT and BTLF displays are presented in Figure 2. The nonaggressive, submissive "move away from" behavior was the most common behavior seen after both BT and BTLF displays (30.4 and 30.5%, respectively). BTLF displays were more frequently preceded by "approach" than BT displays (20.7% vs. 10.3%) and overall occurred more frequently with "approach" at any time than BT displays (30.4% vs. 18.9%). "Stare with lowered head" occurred more frequently after a BT than a BTLF display (12.4% vs. 5.5%).

Both male and female BTLF displays were associated with nonaggressive behaviors at similar frequencies (Table S3). 22.2% of male BTLF displays were preceded by approach and 16.2% occurred during approach, while zero female BTLF displays were preceded by or occurred during approach.

3.3 | Facial display blending

We investigated structural blending between the BT or BTLF, LS, and the EB displays in 759 displays with codable upper face movements. Out of these 759 displays, 25.2% (n = 191) of displays were structural blends involving all essential AUs of more than one parent display (Table 4; Figure 3). The majority (n = 104; 54.5%) of blended displays included the lip-flip. The majority of displays with a lip-flip within this sub-analysis were structurally blended (n = 104 [55.6%]) rather than unblended.

We classified the inferred motivational state of structurally blended displays by co-occurrence with nonaggressive (further specified as affinitive or submissive) and/or aggressive behaviors at any time-point (Table 5). The structurally blended BTLF displays most frequently occurred with unblended behaviors reflecting the established inferred motivational state of the other parent display. The BTLF + LS structural blend occurred most frequently with unblended affinitive motivation (38.3%) and the BTLF + EB structural blend occurred most frequently with unblended aggressive motivation (42.9%) (Table S4).

4 | DISCUSSION

Structurally, we define the gelada lip-flip as an optional expression element added to the BT display because the lip-flip always occurred with the essential AUs that define the BT display. We also establish an overall nonaggressive, and more specifically, submissive inferred motivational state for both the BT and BTLF displays. Furthermore, we conclude that the unique lip-flip may function as a communicative specifier of benign intent after peaceful approach because it seems to add information to the BT display about the increased likelihood of a specific type of nonaggressive behavior (Shannon, 1948). Alternatively, the lip-flip may serve as a signal intensifier due to its increased conspicuousness. For example, the lip-flip occurred with the majority of structurally blended displays and may serve to intensify the signal of the other display component. These results suggest that selection for increased facial mobility in geladas promotes the development of increased communicative complexity though multiple potential mechanisms.

From a behavioral perspective, both the BT and BTLF most frequently occurred with nonaggressive, and specifically submissive, sender behaviors. Moreover, both occurred with significantly fewer aggressive behaviors than the EB display, an established threat display. In addition, a higher frequency of displays that co-occurred with nonaggressive sender behaviors during the display represented BTLF rather than BT displays. We therefore conclude that both the BT and BTLF displays most likely have nonaggressive motivational bases as inferred from sender behaviors only, while the BTLF display may have increased nonaggressive signaling value compared to the BT display. Furthermore, male BT displays were more likely to include the lip-flip than female BT displays, which coincides with sexual dimorphism seen with gelada vocalizations and suggests increased selection for communicative complexity in males (Gustison & Bergman, 2016).

There are several other possible explanations for the differences in inferred motivation between the BT and BTLF displays, reflecting different mechanisms through which increased facial mobility may facilitate increased communicative complexity (Micheletta et al., 2013). The addition of the lip-flip movement to the BT display may reflect an increased intensity of nonaggressive signaling, resulting in the innervation of the lip-flip's sling-like muscle apparatus (Hill, 1969); this would suggest that the gelada bared-teeth display is potentially a graded display with the lip-flip promoting an enhanced nonaggressive signal. Alternatively, the lip-flip may serve as an "alerting component" that increases the conspicuousness of the overall BT display (Krebs & Dawkins, 1984; Maynard Smith & Harper, 2003), potentially making the display more detectable (Dobson, 2009b) or decreasing receiver habituation (Partan & Marler, 2005). Moreover, BTLF displays were significantly more likely to occur with several nonessential AUs compared to the BT display, including AU 16 (lower lip depress), though this only had moderate agreement on reliability testing, and AU 27 (mouth stretch). The addition of these nonessential AUs promoting increased tooth and oral mucosa exposure may also serve to increase display conspicuousness or intensity.

While we propose that the BTLF is a nonaggressive display based upon our sender behavior analysis, it did still occur with aggressive sender behaviors at low frequencies of 5–12%. Geladas may be able to exploit the lip-flip's general nonaggressive motivational basis for frequency-dependent tactical deception (Dawkins & Guilford, 1991). If the receiver is likely to interpret the BTLF as a nonaggressive signal, the sender can infrequently take advantage of the receiver's expected response with unexpectedly aggressive behavior. Moreover, the lip-flip is an essential structural element of the aggressive jaw-fencing activity, but we conservatively excluded these movements from our analysis due to our concern that the lip-flip may be a physiologic component rather than a communicative element of jaw-fencing movements. Similarly, the lip-flip can be produced with yawning; these displays were similarly excluded to promote the most conservative motivational analysis. However, recent studies suggest that certain subtypes of yawns in geladas can be used in aggressive contexts (Leone, Ferrari, & Palagi, 2014). It is therefore possible that these exclusions led to the underestimation of the lip-flip's possible aggressive intent.

The BTLF display also occurred statistically significantly more frequently than the BT display with no associated sender behaviors both during and after the displays. The production of BTLF displays without associated social behaviors and with potentially self-directed behaviors such as yawning (accounting for 21.8% of lip-flip events in this study) supports Dunbar and Dunbar's (1975) conclusion that the lip-flip may sometimes reflect a state of internal uncertainty or crisis. In this setting, the lip-flip movement may result from a motor tick or have a stress-relieving function rather than a communicative function.

In our study, both structural and inferred motivational blending appeared to play a significant role in the gelada facial display repertoire; moreover, the majority of coded blended displays included a lip-flip. Similarly to prior studies of display blending in chimpanzees (Parr et al., 2005), we found that the inferred motivational state of just one of the parent displays most frequently dominated the inferred motivational state of the structurally blended display. A possible explanation is that a motivational conflict produced the structural blending, but the motivation that led to the production of the BTLF was dominated by the motivation of the other parent display (Partan & Marler, 2005). Alternatively, Partan and Marler (2005) also predicted that blending may result in amplified versions of one of the parent displays; blending, in this case, would create more intense signals that could provide more specific information about the intensity of the sender's motivational state. Our study's frequent pattern of motivational dominance by the non-BTLF parent display may therefore reflect the amplification of the dominant parent display's motivation via blending with the conspicuous lip-flip.

4.1 | Limitations

From a structural standpoint, we treated continuous sequences of AUs without pause as single displays. This may have confounded structural and inferred motivational analysis due to the inability to capture the full complexity of the temporal sequence of AUs. Additionally, we did not measure AU intensity, but this may be relevant for motivational analysis. Finally, we utilized a modified version of human FACS rather than a non-human primate version of FACS for structural analysis based upon prior literature precedent. We did not create a gelada-specific FACS, as this was not within the scope of this article, though this would potentially be useful for future studies investigating gelada facial mobility.

From a behavioral standpoint, only sender behaviors could be measured, which likely hindered analysis of the lip-flip's true communicative value. However, our findings that the lip-flip has likely nonaggressive, and specifically submissive, motivations appear consistent with previously reported receiver behavioral responses to the lip-flip. For example, van Hooff (1967) reported decreased aggressive behaviors from approaching dominant individuals in response to a silent bared-teeth display with or without a lip-flip, suggesting that these displays likely serve an appeasing function. Alvarez and Consul (1978) reported that the lip-flip, or "raising lip" display, often occurred in response to greeting or approach from other individuals. Future studies should also explore recipient behaviors as part of the communication dyad for further analysis of signal meaning.

Finally, this study did not explore concurrent vocalization analysis, though multimodal signaling was noted to occur and is likely an important element in communicative complexity (Micheletta et al., 2013; Partan & Marler, 1999; Slocombe, Waller, & Liebal, 2011).

4.2 | Conclusion

The evolution of increased facial mobility in geladas, leading to the development of the unique lip-flip movement, may promote increased communicative complexity and efficacy though multiple mechanisms including signal specification, intensification, and blending. These findings can potentially inform further studies exploring the evolutionary origins of increased communicative complexity leading to human language.

ACKNOWLEDGMENTS

The Claire Garber Goodman Fund from Dartmouth College supported this research. The gelada project was funded by the University of Michigan, the National Science Foundation (NSF-1340911, BCS-0715179, BCS-0962118, IOS-1255974), The Leakey Foundation (multiple awards), and the National Geographic Society (multiple awards). We thank Seth Dobson, Ph.D., for his important role in performing study design, video collection, and preliminary data analysis. We thank the anonymous reviewers for helping to improve earlier versions of this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Stefanie P. Lazow https://orcid.org/0000-0003-1826-842X

REFERENCES

Alvarez, F., & Consul, C. (1978). The structure of social behavior in *Theropithecus gelada*. *Primates*, *19*, 45–59. https://doi.org/10.1007/BF02373226

Bout, N., & Thierry, B. (2005). Peaceful meaning for the silent bared-teeth displays of mandrills. *International Journal of Primatology*, *26*(6), 1215–1228. https://doi.org/10.1007/s10764-005-8850-1

Bramblett, C. A. (1970). Coalitions among gelada baboons. *Primates*, *11*, 327–333. https://doi.org/10.1007/BF01730637

Braune, P., Schmidt, S., & Zimmerman, E. (2008). Acoustic divergence in the communication of cryptic species of nocturnal primates. *BMC Biology*, *6*, 19. https://doi.org/10.1186/1741-7007-6-19

Burrows, A. M. (2008). The facial expression musculature in primates and its evolutionary significance. *BioEssays*, *30*, 212–225. https://doi.org/10.1002/bies.20719

Caeiro, C., Waller, B., Zimmerman, E., Burrows, A., & Davila-Ross, M. (2013). OrangFACS: A muscle-based facial movement coding system for orangutans (pongo spp.). *International Journal of Primatology*, *34*(1), 115–129. https://doi.org/10.1007/s10764-012-9652-x

Corballis, M. C. (2010). Mirror neurons and the evolution of language. *Brain & Language*, *112*, 25–35. https://doi.org/10.1016/j.bandl.2009.02.002

Dawkins, M. S., & Guilford, T. (1991). The corruption of honest signaling. *Animal Behaviour*, *41*, 865–873. https://doi.org/10.1016/S0003-3472(05)80353-7

Dobson, S. D. (2006). *Comparative study of facial mobility in anthropoid primates (Unpublished doctoral dissertation)*. St. Louis, MO: Washington University in St. Louis.

Dobson, S. D. (2009a). Allometry of facial mobility in anthropoid primates: Implications for the evolution of facial expression. *American Journal of Physical Anthropology*, *138*, 70–81. https://doi.org/10.1002/ajpa.20902

Dobson, S. D. (2009b). Socioecological correlates of facial mobility in nonhuman anthropoids. *American Journal of Physical Anthropology*, *139*, 413–420. https://doi.org/10.1002/ajpa.21007

Dunbar, R. I. M., & Dunbar, P. (1975). Social dynamics of gelada baboons. In *Contributions to primatology* (Vol. 6). Basel, NY: Karger.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002). *Facial action coding system: The manual on CD-ROM*. Salt Lake City, UT: Research Nexus.

Fedigan, L. M. (1972). Roles and activities of male geladas (*Theropithecus gelada*). *Behaviour*, *41*, 82–90. https://doi.org/10.1163/156853972X00211

Freeberg, T. M. (2006). Social complexity can drive vocal complexity: Group size influences vocal information in Carolina chickadees. *Psychological Science*, *17*, 557–561. https://doi.org/10.1111/j.1467-9280.2006.01743.x

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B*, *367*, 1785–1801. https://doi.org/10.1098/rstb.2011.0213

Gamba, M., Friard, O., & Giacoma, C. (2012). Vocal tract morphology determines species-specific features in vocal signals of lemurs (Eulemur). *International Journal of Primatology*, *33*(6), 1453–1466. https://doi.org/10.1007/s10764-012-9635-y

Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews*, *30*(7), 949–960. https://doi.org/10.1016/j.neuobiorev.2006.02.004

Ghazanfar, A. A., & Takahashi, D. Y. (2014). Facial expressions and the evolution of the speech rhythm. *Journal of Cognitive Neuroscience*, *26*(6), 1196–1207. https://doi.org/10.1162/jocn_a_00575

Gustison, M. L., & Bergman, T. J. (2016). Vocal complexity influences females responses to gelada male calls. *Scientific Reports*, *6*, 19680. https://doi.org/10.1038/srep19680

Hill, W. C. O. (1969). On the muscles of expression in the gelada *Theropithecus gelada* (Rüppell) (primates, Cercopithecidae). *Zoomorphology Tiere*, *65*, 274–286.

Kawai, M. (1979). Auditory communication and social relations. In M. Kawai (Ed.), *Ecological and sociological studies of gelada baboons: Contributions to primatology* (Vol. 16, pp. 219–242). Tokyo: Kodansha Ltd..

Kawai, M., Ohsawa, H., Mori, U., & Dunbar, R. (1983). Social organization of gelada baboons: Social units and definitions. *Primates*, *24*, 13–24.

Kean, D., Tiddi, B., Fahy, M., Heistermann, M., Schino, G., & Wheller, B. C. (2017). Feeling anxious? The mechanisms of vocal deception in tufted capuchin monkeys. *Animal Behaviour*, *130*, 37–46. https://doi.org/10.1016/j.anbehav.2017.06.008

Krebs, J. R., & Dawkins, R. (1984). Animal signals: Reading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd ed., pp. 380–402). Oxford: Blackwell.

Kroodsma, D. E. (1977). Correlates of song organization among North American wrens. *The American Naturalist*, *111*(9831), 995–1008 DOI.org/10.1086/283228.

Leone, A., Ferrari, P. F., & Palagi, E. (2014). Different yawns, different functions? Testing social hypotheses on spontaneous yawning in *Theropithecus gelada*. *Scientific Reports*, *4*, 4010. https://doi.org/10.1038/srep04010

Marler, P. (1965). Communication in monkeys and apes. In I. DeVore (Ed.), *Primate behavior: Field studies of monkeys and apes* (pp. 544–584). New York, NY: Holt, Rinechart, and Winston.

Maynard Smith, J., & Harper, D. (2003). *Animal signals*. Oxford: Oxford University Press.

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*, 381–385. https://doi.org/10.1098/rsbl.2005.0366

Micheletta, J., Engelhardt, A., Matthews, L., Agil, M., & Waller, B. (2013). Multicomponent and multimodal lipsmacking in crested macaques (*Macaca nigra*). *American Journal of Primatology*, *75*(7), 763–773. https://doi.org/10.1002/ajp.22105

Mori, U. (1979a). Individual relationships within a unit. In M. Kawai (Ed.), *Ecological and sociological studies of gelada baboons: Contributions to primatology* (Vol. 16, pp. 93–124). Tokyo: Kodansha Ltd..

Mori, U. (1979b). Reproductive behavior. In M. Kawai (Ed.), *Ecological and sociological studies of gelada baboons: Contributions to primatology* (Vol. 16, pp. 183–199). Tokyo: Kodansha Ltd..

Parr, L. A., Cohen, M., & de Waal, F. (2005). Influence of social context on the use of blended and graded facial displays in chimpanzees. *International Journal of Primatology*, *26*, 73–103. https://doi.org/10.1007/s10764-005-0724-z

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

Parr, L. A., Waller, B. M., & Micheletta, J. (2016). Nonverbal communication in primates: Observational and experimental approaches. In D. Matsumoto, H. C. Hwang, & M. G. Frank (Eds.), *APA handbook of nonverbal communication*. Washington, D.C.:American Psychological Association.

Parr, L., & Waller, B. M. (2006). Understanding chimpanzee facial expression: Insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*, *1*, 221–228. https://doi.org/10.1093/scan/nsl031

Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action. *Emotion*, *7*, 172–181. https://doi.org/10.1037/1528-3542.7.1.172

Partan, S. R., & Marler, P. (1999). Communication goes multimodal. *Science*, *283*, 1272–1273. https://doi.org/10.1126/science.283.5406.1272

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, *166*, 231–245. https://doi.org/10.1086/431246

Scheider, L., Liebal, K., Ona, L., Burrows, A. M., & Waller, B. M. (2014). A comparison of facial expression properties in five hylobatid species. *American Journal of Primatology*, *76*(7), 618–628. https://doi.org/10.1002/ajp.22255

Shannon, C. E. (1948). A mathematical theory of communication. *Bell Labs Technical Journal*, *27*, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Slocombe, K. E., Waller, B. M., & Liebal, K. (2011). The language void: The need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/10.1016/j.anbehav.2011.02.002

Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012). Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). *International Journal of Primatology*, *33*, 1054–1068.

Thierry, B., Demaria, C., Preuschoft, S., & Desportes, C. (1989). Structural convergence between silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia Primatol (Basel)*, *52*(3–4), 178–184. https://doi.org/10.1159/000156396

van Hooff, J. A. R. A. M. (1967). The facial displays of catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). Chicago, IL: Aldine Publishing Company.

Viera, A. J., & Garrett, J. M. (2005). Understanding interobserver agreement: The kappa statistic. *Family Medicine*, *37*(5), 360–363 PMID: 15883903.

Waller, B., Lembeck, M., Kuchenbuch, P., Burrows, A., & Liebal, K. (2012). GibbonFACS: A muscle-based facial movement coding system for hylobatids. *Internal Journal of Primatology*, *33*(4), 809–821. https://doi.org/10.1007/s10764-012-9611-6

Waller, B. M., & Michelatta, J. (2013). Facial expression in nonhuman animals. *Emotion Review*, *5*(1), 54–59. https://doi.org/10.1177/1754073912451503

Waller, B. M., Warmelink, L., Liebal, K., Michelatta, J., & Sclocombe, K. E. (2013). Pseudoreplication: A widespread problem in primate communication research. *Animal Behaviour*, *86*(2), 483–488.

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

Zimmerman, E. (2017). Evolutionary origins of primate vocal communication: Diversity, flexibility, and complexity of vocalizations in basal primates. In R. M. Quam, M. A. Ramsier, R. R. Fay, & A. N. Popper (Eds.), *Primate hearing and communication* (pp. 109–140). Berlin, Germany: Springer. https://doi.org/10.1007/978-3-319-59478-1_5

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Lazow SP, Bergman TJ. The structural and motivational role of the unique lip-flip movement in the gelada (*Theropithecus gelada*) facial display repertoire. *Am J Phys Anthropol*. 2020;172:280–290. https://doi.org/10.1002/ajpa.24031