# Female Diana Monkeys have Complex Calls

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Recent literature on non-human animal communication has unearthed call combinations that appear to follow internal rules of composition (e.g., Coye et al. 2015, 2016, Dutour et al., 2019, Suzuki et al., 2016, Suzuki and Matsumoto, 2022). Specifically, various studies have found a rudimentary, non-recursive operation that allows the combination of two atomic units; this is sometimes referred to as 1-Merge in a typology proposed by Rizzi (2016). Some of these combinatorial systems have been analyzed with tools from formal linguistics. These include call combinations found in Putty-nosed monkeys (Schlenker et al., 2016a), Titi monkeys (Berthet et al., 2019), as well as the *-oo* suffix in the alarm call system of Campbell's monkeys, an early example initially discussed by Ouattara et al. (2009), and further investigated by Kuhn et al. (2014) and Schlenker et al. (2014). The *-oo* suffix can be optionally attached to the root alarm calls *hok* and *krak*, modifying the root's meaning into that of a less urgent alarm.

In the present paper, we study the A call, found in female Diana monkeys (Cercopithecus diana), with a close counterpart in female Campbell's monkeys (Cercopithecus campbelli). We argue that the A call can be combined with other calls to form complex units. We reject (on both empirical and conceptual grounds) a combination-free analysis based on accidental homophony, and we consider two main analyses: the Acoustic Theory takes the combination to be merely acoustic, whereas the Affixal Theory takes A to function as a suffix. We provide limited arguments for the Affixal Theory, and through comparison with another closely related monkey species, we date these combinations to at least 6 million years ago.

#### 1. Contact call system of female Diana Monkeys

We will focus on four basic call types of female Diana monkeys, which Candiotti et al., (2012a) studied and associated with rules of use<sup>1</sup>: H, L and R units relate to the context of emission while A calls strongly convey caller's identity (Candiotti et al., 2012b, Coye et al., 2022), as summarized in Table 1. More details about the calls' usage and example spectrograms can be found in Candiotti et al. (2012a,b) and Coye et al. (2016, 2022).

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<sup>&</sup>lt;sup>1</sup> We will not refer to, or discuss, the semantics in this paper, instead only referring to the calls' rules of use as determined by the observer's description of the contexts in which calls are used.

**Table 1** Simple acoustic descriptions and rules of use for the basic call types of Diana Monkeys, according to Candiotti et al. (2012a).

Call	Acoustic description	Rules of use
L	low-pitched trill	used if the caller is in a neutral affective state
Н	high-pitched trill	used if the caller is in a positive affective state
R	repeated unit call (broadband)	used if the caller is in a negative affective state
A	arched frequency-modulated calls (with 2 subtypes: (i) Abbroken arch, (ii) Af-full arch)	used to advertise caller's identity and social bonds (Af is preferentially used when conveying identity is particularly important)

These calls are produced in isolation or in sequences. Within these sequences, Candiotti et al. show that a restricted set of call combinations can appear *without* an observable pause between the call subparts. These combinations are given in (1); we will refer to them as Blended Bigrams:<sup>2</sup>

### (1) Blended Bigrams:

- a. LA
- b. HA
- c. RA

At the semantic level, which we will not investigate in any detail, the available data do not provide evidence for anything but conjunctive meanings for these Blended Bigrams: two concatenated calls C C' are licensed just in case each of them is (and thus, semantically, no non-trivial rule of combination is required). Specifically, Candiotti et al. show that any call XA (where X stands for L, H, or R) is arguably restricted in use to the contexts in which the call X alone can be appropriately used; this is of course compatible with a conjunctive meaning. In addition, Coye et al. (2016) showed in a playback experiment that changing one unit in a combination (e.g., L to R, thus moving LA to RA) significantly alters receivers' behavior, towards a response appropriate for the target change (e.g., reacting as if a regular RA had been used).

### 2. Three hypotheses

The Blended Bigrams can be analyzed in three ways. The first hypothesis ('Accidental Homophony') posits that LA, HA and RA are elementary calls that happen to be homophonous with call combinations. This posits three accidental homophonies, and we thus take this theory to lack explanatory depth. We will set it aside for the time being, but we will show in Section 5 that it fails to account for a key distributional pattern.

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 $<sup>^2</sup>$  For all calls, the use of both subtypes of A has been observed. However, while  $HA_b$  and  $RA_b$  calls are in the dataset, these calls have not been taken into account in the analysis due to small sample size and because they were never given as part of a sequence. In the main text, we will not distinguish between  $A_b$  and  $A_f$  calls, unless it is strictly necessary.

The second hypothesis ('Acoustic Theory') posits that the Blended Bigrams are regular bigrams, made of two simple calls, which happen to be pronounced in close succession. This might be attributed to a general tendency to pronounce calls in close succession whenever this is possible on acoustic (and possibly articulatory) grounds.

# (2) Acoustic Theory

- a. Roots: L, H, R, A
- b. **Lexicon:** Every root is a word.
- c. **Maximize Adjacency rule:** For any two words X and Y uttered in sequence, X and Y have to be acoustically maximally adjacent.

The third hypothesis is that the Blended Bigrams are effectively words, i.e. they are made of morphemes that follow rules of combinations. The semantic rule of combination may be mere conjunction (see above), while the rules of word formation could be as described in (3). The Blended Bigrams are thus words, composed of two parts, X and A, where X is a non-A-type (L, H, or R) root, and A is a bound morpheme (a suffix).<sup>3,4</sup>

### (3) Affixal Theory

- a. Roots: L, H, R, A
- b. Affix: A
- c. Lexicon:
  - i. Every root is a word.
  - ii. For every root X different from A, XA is a word.

In the Affixal Theory, the rules governing how calls are composed are distinct from the rules governing how sequences of calls are composed; in this sense, these are rules of Diana monkey 'morphology'.<sup>5</sup>

The Acoustic and the Affixal Theories are empirically close. We will review arguments that could help evaluate them. The main types of arguments are as follows. (i) First, the maximal length of call sequences (§4.1) and patterns of repetitions (§4.2) support the idea that XA combinations indeed behave as units; these are naturally thought of as morphological units (words), or as acoustic units. (ii) The Affixal Theory explains better than the Acoustic Theory which combinations of calls may or may not appear without pauses, and a more general tendency for A calls to appear early in call sequences. Crucially, the Accidental Homophony theory fails in this respect (§4.3). Finally, (iii) a closely related species, Campbell's monkeys (*Cercopithecus campbelli*), has a counterpart of A, and only

<sup>&</sup>lt;sup>3</sup> Here we have to grant that, given the fact that the Diana monkeys' repertoire is extremely limited, we cannot show that the rule of complex word formation is productive (a similar caveat applied to the analysis of *-oo* as a suffix in Campbell's monkeys, Schlenker et al. 2014).

<sup>&</sup>lt;sup>4</sup> A-type calls having a double life as both roots and affixes would be analogous to how we see *able* and *-able* behaving in English (as in *Most people are able to walk in my neighborhood* vs. *My neighborhood is walkable for most people*).

<sup>&</sup>lt;sup>5</sup> In line with Schlenker et al. (2014), (i) we sometimes apply linguistic terminology to monkey call systems because we think these should be studied as formal languages, just like human language, but (ii) we emphatically do not make any claims about their relation to human language.

uses it as a suffix (§4.4), which dovetails with its suffixal use in Diana monkeys, and the use of the -oo suffix by the males of this species.

#### 3. Dataset

This paper presents an analysis of the data from Candiotti et al. (2012a). Data collection took place between 7.30am and 5pm on two groups of Diana monkeys habituated to the presence of human observers. The observer followed an adult female for 10 minutes at a time and females were followed in a pseudo-random order over the day. Calls from the focal individual were recorded using a Sennheiser K6/ME66 directional microphone and a Marantz PMD660 solid-state recorder (sampling rate, 44.1 kHz; resolution, 16 bits).

The data consist of 2,427 calls collected from the Taï National Park (Ivory Coast) between December 2009 and June 2010. The recordings were divided into 2,021 sequences, assuming that a pause longer than 2 seconds marks the end of a sequence. This threshold was chosen following standard practice and the analysis of the distribution of pause duration (there were many pauses lasting for 2 seconds or less, and passed this threshold there was a somewhat uniform, but smaller, number of pauses lasting between 3 and 60 seconds).

### 4. Comparing Theories

We turn to the empirical arguments that can help adjudicate among theories. Overall, they show that XA calls behave like units, be they morphological or acoustic (or homophony-based) (§5.1 and §5.2). Further facts about word order are easier to incorporate in the Affixal Theory (§5.3). We also discuss (§5.4) an additional argument for treating the A-type call as an affix, based on the comparison of the repertoires of female Diana monkeys and female Campbell's monkeys.

# 4.1. Maximal Sequence Length is Best Counted in Numbers of (Simple or Complex) Units

The dataset shows that there is a limit on sequence length (i.e. maximal number of calls uttered in a given sequence). Looking first at sequences that consist solely of simple calls, such as (4a) and (4b) below, we see that none of them exceeds five calls in length. Second, when we look at *all* the sequences, the same upper bound of 5 applies, but only if we count a Blended Bigram as one unit (see, e.g., (4c), which contains 5 *pairs* of elementary units).

### (4) Examples of maximally long sequences

a. A A A A A
 b. R R R R
 c. LA LA LA LA LA
 d. A A LA LA
 e. H LA HA HA
 f. LA LA LA H LA

This generalization shows that there is structure in these sequences, based on intermediate units which are either words—in the Affixal Theory—or phonological units<sup>6</sup>

<sup>6</sup> To draw a parallel with human languages here, the modified Phonological Theory positing that calls such as LA are not morphosyntactic words, but are phonological units, could be seen as akin to cliticization, where A is encliticizing onto the root L. But in any event, the notion of 'phonological unit' used here needs to be stipulated in the case at hand; its sole motivation is to yield the right limit on sequence length.

-in the Acoustic Theory (we note for future reference that this generalization can also be captured by the Accidental Homophony theory, for which XA is just an elementary call). An alternative is that there is an independent explanation for the length constraint, e.g., one based on sequence duration. We do not investigate this possibility further, and instead move to other arguments.

### 4.2. Repetition Targets (Simple or Complex) Units

To explore repetition patterns in sequences of (basic and complex) calls, we analyzed call co-occurrence in sequences using the method that Frisch et al. (2004) employed to analyze constraints on consonant clusters in Arabic. This method compares the observed frequency of bigrams to the one expected if the calls were randomly combined. The aim is to determine which bigrams, if any, are preferentially used, and which are used less frequently than expected. The expected frequency of a call bigram is the product of base frequencies of the two calls that form the bigram in the positions in which they are found, multiplied by the total number of bigrams. The result is the number of bigrams of a given composition that would be expected if its individual calls were to be combined at random. The observed bigram frequency is divided by the expected value, giving the observed over expected (O/E) bigram frequencies, shown in Table 2. For any given bigram, the O/E value of 1 indicates at-chance distribution. Values lower than 1 indicate a lower than expected number of bigrams, and thus the existence of a constraint on the use of a bigram. Values higher than 1 indicate a greater than expected number of bigrams, suggesting preferential use.

The first result is that repetitions, i.e. adjacent co-occurrences of identical units, are frequent: the values in the diagonal are high (above 1, and higher than outside of the diagonal). This is unsurprising: call repetition has been noted in the repertoires of Campbell's monkeys (see Schlenker, et al., 2014 for examples of sequences), Blue monkeys (Fuller, 2012), and Putty-Nosed monkeys (Arnold & Züberbuhler, 2006).

**Table 2**Co-occurrence of call types in sequences. The rows mark the first call of the bigram and the columns the second. For instance, bigrams H L are accounted for in the cell in row marked with H, and the column marked with L.

	Ab	Af	Н	HAf	L	LAb	LAf	R	RAf
Ab	4.4	0.6	0.7	0.0	1.6	0.4	0.6	0.0	0.5
Af	0.8	3.3	0.6	0.0	0.3	0.2	0.3	0.0	1.5
н	0.0	0.0	3.6	0.0	0.0	1.4	1.3	0.0	1.8
HAf	0.0	0.0	4.5	47.4	0.0	0.0	1.1	0.0	0.0
L	0.0	0.0	0.0	0.0	17.5	0.0	0.9	0.0	0.0
LAb	0.4	0.3	0.8	0.0	3.2	4.1	0.7	0.0	0.6
LAf	0.2	0.2	1.2	1.2	0.2	0.8	1.7	0.0	0.4
R	0.0	0.0	0.0	0.0	0.0	0.0	0.0	126.3	0.0
RAf	1.0	0.5	0.0	0.0	0.0	0.0	0.7	0.0	12.0

The second, important result is that repetition also targets Blended Bigrams (HA-HA for instance receives an index of 47.4, way above 1). This shows that these Blended Bigrams are treated as complex units from the point of view of repetition. This lends itself to the following accounts in the Affixal and Acoustic Theories:

- (5) **Repetition in the Affixal Theory:** Words may be repeated.
- (6) **Repetition in the Acoustic Theory:** Acoustic units may be repeated.<sup>7</sup>

A third key result is that repetition does not target the A call alone when it appears as a part of these complex units ("HA\_A", "LA\_A", "RA\_A" receive low values in Table 2). In the Affixal Theory, this is not a necessary fact, but quite a natural one: a suffix cannot easily be repeated, as an affix. In the Acoustic Theory, one could more easily imagine ways in which a unit that ends up realized as part of an acoustic unit may be later repeated and therefore appear in its own acoustic unit.

This might yield an initial advantage to the Affixal Theory, but more conservatively, this is at least additional evidence that the Blended Bigrams in (1) should be treated as complex, natural units: words or phonological units. (We note for future reference that all three results can be captured by the Accidental Homophony theory, since it treats LA, HA and RA as elementary calls, not containing the A call/suffix.)

### 4.3. Combinations of X's and A's Calls with a Pause

While we focused so far on call sequences made of X's and A's without a pause, we now look at such combinations with pauses, notated as \_. While the facts require auxiliary hypotheses, they will give an advantage to the Affixal Theory. The facts are as follows:

First, the existence of A\_X, A\_A and X\_X sequences is a challenge for the Acoustic Theory. This theory posits that pauses are dispreferred, and it would thus have to specify some constraints, for instance of an articulatory nature, that prevents some combinations from being merged (but not X and A in this order). For the Affixal Theory, this follows from the assumption that the X's are not affixes (A\_X and X\_X), and that A does not combine with A. Why this is so should in the end be explained, although arbitrariness is a standard feature of morphology.

Second, and conversely, the Acoustic Theory accounts for the absence of (7d), as the theory was designed to do so: pauses should be avoided if at all possible. For the Affixal Theory, this must follow from an additional principle. One simple possibility is that the sequence  $X_A$  does not appear because it competes with the single word XA, and XA wins (which is made plausible by the fact that the two may be semantically equivalent, or other

<sup>7</sup> The Phonological Theory could also postulate that repetition targets simple units, but then it would not explain why Blended Bigrams are frequently repeated. It may postulate instead that repetition targets either units or combinations of units, but then it would overgenerate: sequences of the type "A L A L" are unattested, while sequences like "A L" exist.

potential instances of similar competition principles in other species such as the Urgency Principle, Schlenker et al., 2016a).

Importantly, one may also ask whether the ban against X\_A may be part of a broader generalization, e.g., one which makes A roots appear early in the sequences, and therefore not appear *after* X's (or anything else). Upon examining the sequences, we see that 116 sequences of the 273 sequences of two or more calls start with an A (42.4% of the sequences). However, there are only 236 instances of A calls in the 680 calls of these multicall sequences (34.7%). So, among these As, 48.2% occur in the initial position. And the A's that do not occur in initial position are in fact always preceded by another A call or XA call. The generalization, which we call "Identity First" because A conveys individual identity more strongly than any other call type (see section 2), is thus as follows:

### (8) Identity First:

For any sequence S, if S contains the root A, A cannot be preceded by any call other than one with the root or the affix A.

A possible explanation for this "Identity First" pattern lies in the limited visibility in Diana monkeys' environment, which may make the need to signal one's identity from the start of the vocal sequence particularly important. The fact that some calls carry identity more than others has been studied in several species, see Charrier et al., 2001; Lemasson & Hausberger, 2011; Rendall et al., 2009).

Crucially, the generalization in (8) relies on the analysis offered by the Affixal Theory: XA must be treated as a single call. Otherwise, as in the Acoustic Theory one cannot incorporate (8), as every complex call XA will be analyzed as a sequence of two calls in which A is non-initial. Thus, although both theories account for the unattested call combination with a pause  $X_A$ , the Affixal Theory can account for it by making it part of a broader pattern, which escapes the Acoustic Theory.

Throughout our discussion, we backgrounded the Accidental Homophony Theory because it lacks explanatory depth, yet granting in passing that it can account for the main findings so far. But there is now an empirical argument against it because it has no easy way of accounting for (7)d, namely the absence of X\_A: since it takes XA to be unrelated to X and A, neither pause minimization nor competition can explain the absence of X\_A. Accidental Homophony lacks explanatory depth, but in addition it fails to account for an important generalization.

# 4.4. An Argument From the Homologous Call of the Female Campbell's Monkeys

The argument that A can be used as both a root and a suffix, and could thus be constrained differently by syntactic rules, is further supported by the data from female Campbell's monkeys. The Diana and Campbell's monkeys are closely related species (last common ancestor: about 6 MYA, Perelman et al., 2011). They share the same visually restricted habitat and a similar social structure with one adult male emitting alarm calls only and several females forming the social core of the group (Whitesides, 1989, Rowe, 1996). Diana and Campbell's female monkeys rely on numerous homologous calls, both in terms of acoustic structure and function (Coye et al., 2022, 2018, Candiotti et al., 2015, Lemasson & Hausberger, 2011). Specifically, they share homologous threat calls, alarm calls and several types of social calls. The relevant ones are given in Table 3. They include the three types of "X calls" (H, L and R) and both "A calls" subtypes (Af and Ab). The vocal

repertoires of non-human primates are under strong genetic influences and generally reflect phylogeny (Geissmann, 1984; Ord & Garcia-Porta, 2012). For instance, Gautier et al. (1988, 1989) were able to reconstruct the phylogeny of guenons based on their calls. It is thus likely that the calls shared by the two species were inherited from a common ancestor.

**Table 3**Function, names and acoustic structure of the homologous calls in Diana and Campbell's female monkeys

Call function	Diana Monkeys Call name	Campbell's Monkeys Call name	Acoustic structure
Alarm call	R	RRA	Broadband repetitive unit
Social context (neutral)	L	SH	Low-pitched trills
Social context (positive)	Н	ST	High-pitched, descending trills
Contact calls	LAf and LAb	CHf and CHb	Combined structure composed of an SH/L unit and an arched unit (i.e. A units in Diana Monkeys)

Interestingly, while Diana females can utter all X and A calls alone or in XA combinations, call use in Campbell's monkeys is narrower: Campbell's females can use all their X calls alone, but they can only use their A calls as affixes following the L-type call (i.e. they can only produce homologous calls to LA but not to A, RA or HA calls). In other words, the suffixal status of Campbell's monkeys' version of A is relatively easy to establish since A does not occur as a standalone call. Given the existing data, we cannot determine whether Diana monkeys diversified their use of A units after the split or whether Campbell's monkeys lost that ability. However, we can plausibly infer that the affixed A-type calls were present in the common ancestor of these two species, and that both species can use it as a suffix, while Diana monkeys may also use it as a root.

#### 5. Conclusion

We have provided evidence that the A call of Diana monkeys (and a homologous form in Campbell's monkeys) is used to construct complex units, whether words or acoustic units. Specifically, the Affixal Theory posits that the social *A-type* call of Diana monkeys can be used both as a suffix and as a root, with different rules affecting their distribution. This theory makes it natural to express generalizations about constraints on sequence length (§5.1), repetition (§5.2) and, better than other theories, about the early appearance of A calls in sequences (§5.3). A deflationary theory in terms of Accidental Homophony lacks explanatory depth, and also fails to account for distributional patterns that involve competition between combinations of the for XA with and without pauses. Finally, the Affixal Theory is supported by recent studies comparing the calls of female Diana monkeys

and female Campbell's monkeys, which have an affixal use for the homologue of the *A-type* call without having an *A-type* root call (§5.4), and whose males have an *-oo* suffix.

We therefore offer a new type of evidence for the existence of a (highly limited) morpho-syntactic rule in animals, an instance of 1-merge as discussed by Rizzi (2016). One may ask whether other instances of call combinations can be found. For instance, there is anecdotal evidence in Diana monkeys of other calls, Alk and W, that seem to occur either in isolation or combined with the R root (see description in Coye et al., 2022). We lack recordings of these calls in sequences, but a complete analysis in the future could reveal a complex morphological system in Diana monkeys. Overall, the current results dovetail with discussions in Collier et al. (2014). We can further speculate that the combinatorial rule involving the A suffix may have arisen in the common ancestor of Diana monkeys and Campbell's monkeys, more than 6M years ago.

#### References

- Arnold, Kate, and Klaus Zuberbühler. 2006. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behavior* 72: 643-653. https://doi.org/10.1016/j.anbehav.2005.11.017
- Berthet, Mélissa, Geoffrey Mesbahi, Aude Pajot, Cristiane Cäsar, Christof Neumann, and Klaus Zuberbühler. 2019. Titi monkeys combine alarm calls to create probabilistic meaning. *Science Advances* 5(5): eaav3991. https://doi.org/10.1126/sciadv.aav399
- Candiotti, Agnes, Klaus Zuberbühler, and Alban Lemasson. 2012a. Context-related call combinations in female Diana monkeys. *Animal cognition* 15: 327-339. https://doi.org/10.1007/s10071-011-0456-8
- Candiotti, Agnes, Klaus Zuberbühler, and Alban Lemasson. 2012b. Convergence and divergence in Diana monkey vocalizations. *Biology Letters* 8(3): 382-385. https://doi.org/10.1098/rsbl.2011.1182
- Candiotti, Agnès, Camille Coye, Karim Ouattara, Eric J. Petit, Dominique Vallet, Klaus Zuberbühler, and Alban Lemasson. 2015. Female bonds and kinship in forest guenons. *International Journal of Primatology* 36: 332-352. https://doi.org/10.1007/s10764-015-9829-1
- Charrier, Isabelle, Pierre Jouventin, Nicolas Mathevon, and Thierry Aubin. 2001. Individual identity coding depends on call type in the South Polar skua Catharacta maccormicki. *Polar Biology* 24: 378-382. https://doi.org/10.1007/s003000100231
- Collier, Katie, Balthasar Bickel, Carel P. van Schaik, Marta B. Manser, and Simon W. Townsend. 2014. Language evolution: syntax before phonology? *Proceedings of the Royal Society B: Biological Sciences* 281(1788): 20140263. https://doi.org/10.1098/rspb.2014.0263
- Coye, Camille, Karim Ouattara, Klaus Zuberbühler, and Alban Lemasson. 2015. Suffixation influences receiver's behaviour in non-human primates. *Proceedings of the Royal Society B: Biological Sciences* 282(1807): 20150265. https://doi.org/10.1098/rspb.2015.0265
- Coye, Camille, Klaus Zuberbühler, and Alban Lemasson. 2016. Morphologically structured vocalizations in female Diana monkeys. *Animal Behaviour* 115: 97-105. https://doi.org/10.1016/j.anbehav.2016.03.010
- Coye, Camille, Karim Ouattara, Malgorzata E. Arlet, Alban Lemasson, and Klaus Zuberbühler. 2018. Flexible use of simple and combined calls in female Campbell's monkeys. *Animal Behaviour* 141: 171-181. https://doi.org/10.1016/j.anbehav.2018.05.014
- Coye, Camille, Klaus Zuberbühler, and Alban Lemasson. 2022. The evolution of vocal communication: Inertia and divergence in two closely related primates. *International Journal of Primatology* 43(4): 712-732. https://doi.org/10.1007/s10764-022-00294-y

<sup>8</sup> Collier et al. (2014) also argue against the existence of phonology in animals, hence against duality of patterning in animals, Hockett (1960).

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- Dutour, Mylène, Thierry Lengagne, and Jean-Paul Léna. 2019. Syntax manipulation changes perception of mobbing call sequences across passerine species. *Ethology*, 125(9): 635-644. https://doi.org/10.1111/eth.12915
- Frisch, Stefan A., Janet B. Pierrehumbert, and Michael B. Broe. 2004. Similarity avoidance and the OCP. *Natural language and linguistics theory* 22: 179-228. https://doi.org/10.1023/B:NALA.0000005557.78535.3c
- Fuller, James. 2012. Diversity of form, content and function in the vocal signals of adult male blue monkeys (Cercopithecus mitis stuhlmanni): an evolutionary approach to understanding a signal repertoire. Ph.D. Dissertation, Columbia University, New York, NY.
- Gautier, Jean Pierre. 1988. Inter-specific affinities among guenons as deduced from vocalizations. *A primate radiation-evolutionary biology of the African guenons*.
- Gautier, Jean Pierre. 1989. A redrawn phylogeny of guenons based upon their calls—Biogeographical implications. *Bioacoustics* 2(1): 11-21.
- Geissmann, Thomas. 1984. Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (Hylobates pileatus× H. lar). *Folia Primatologica* 42(3–4): 216-235.
- Hockett, Charles F. 1960. The origin of speech. Scientific American 203: 88-96.
- Kuhn, Jeremy, Sumir Keenan, Kate Arnold, and Alban Lemasson. 2014. On the -oo suffix of Campbell's monkeys (C. Campbelli). Unpublished manuscript. Retrieved from http://www.jeremykuhn.net/papers/Kuhn-oo-suffix-10-2014.pdf
- Lemasson, Alban, and Martine Hausberger. 2011. Acoustic variability and social significance of calls in female Campbell's monkeys (Cercopithecus campbelli campbelli). *Journal of the acoustic society of America* 129(5): 3341-3352. https://doi.org/10.1121/1.3569704
- Ord, Terry J., and Joan Garcia-Porta. 2012. Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1597): 1811-1828. https://doi.org/10.1098/rstb.2011.0215
- Ouattara, Karim, Alban Lemasson, and Klaus Züberbuhler. 2009. Campbell's monkeys use affixation to alter call meaning. *PLoS ONE* 4: 11. https://doi.org/10.1371/journal.pone.0007808
- Perelman, Polina, Warren E. Johnson, Christian Roos, Hector N. Seuánez, Julie E. Horvath, Miguel AM Moreira, Bailey Kessing et al. 2011. A molecular phylogeny of living primates. *PLoS Genetics* 7(3): e1001342. https://doi.org/10.1371/journal.pgen.1001342. https://doi.org/10.1371/journal.pgen.1001342
- Rendall, Drew, Hugh Notman, and Michael J. Owren. 2009. Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. *The Journal of the Acoustical Society of America* 125(3): 1792-1805. https://doi.org/10.1121/1.3068453
- Rizzi, Luigi. 2016. Monkey morpho-syntax and merge-based systems. *Theoretical Linguistics* 42(1–2): 139-145. https://doi.org/10.1515/tl-2016-0006. https://doi.org/10.1515/tl-2016-0006 Rowe, Noel. 1996. The pictorial guide to the living primates. East Hampton, NY: Pogonios Press.
- Schlenker, Philippe, Emmanuel Chemla, Kate Arnold, Alban Lemasson, Karim Ouattara, Sumir Keenan, Claudia Stephan, Robin Ryder, and Klaus Zuberbühler. 2014. Monkey semantics: Two 'dialects' of Campbell's monkey alarm calls. *Linguistics and Philosophy* 37(6): 439-501. https://doi.org/10.1007/s10988-014-9155-7
- Schlenker, Philippe, Emmanuel Chemla, Kate Arnold, and Klaus Zuberbühler. 2016. Pyow-hack revisited: Two analyses of putty-nosed monkey alarm calls. *Lingua* 171: 1-23. https://doi.org/10.1016/j.lingua.2015.10.002
- Suzuki, Toshitaka N., David Wheatcroft, and Michael Griesser. 2016. Experimental evidence for compositional syntax in bird calls. *Nature communications* 7(1): 10986. https://doi.org/10.1038/ncomms10986
- Suzuki, Toshitaka N., and Yui K. Matsumoto. 2022. Experimental evidence for core-Merge in the vocal communication system of a wild passerine. *Nature Communications* 13(1): 5605. https://doi.org/10.1038/s41467-022-33360-3
- Whitesides, George H. 1989. Interspecific associations of Diana monkeys, Cercopithecus Diana, in Sierra Leone, West Africa: Biological significance or chance. *Animal Behavior* 37: 760-776. https://doi.org/10.1016/0003-3472(89)90062-6