Emotional contexts influence vocal individuality in ungulates

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Abstract

To group-living animals, such as most ungulates, being able to recognise the members of one's

social groups is crucial. While vocalisations often carry cues to identity, they are also impacted

by the affective state of the caller, with signals often becoming more chaotic in contexts of

negative valence or high arousal. How might this influence vocal individuality – and is there a

pattern across taxa? To understand how the individual information content is maintained over

emotionally charged contexts, we studied putatively negative and positive contact calls of seven

ungulate species: cattle, goats, sheep, pigs, wild boars, horses, and Przewalski's horses. Calls

were classified to individuals using linear and machine learning methods, and their information

content assessed using Beecher's statistic and the Potential of Individuality Coding. In most

species, calls could be reliably classified to the caller within and across affective states. While

there was no uniform pattern in information content change between valences across species,

some species showed a pronounced increase in individuality in either positive or negative

situations. In each of the species, at least one acoustic parameter was a reliable indicator of

individuality across contexts. Our results suggest that different coding strategies may be present

across taxa, and imply that individual vocal recognition requires acoustic stability of certain

important parameters. These findings reveal a nuanced role of affective communication in

maintaining social bonds among socially complex animals.

Introduction

In many types of social groups (e.g. family and extended family groups), some form of individual recognition is needed to achieve a good functioning of daily tasks (Ward & Webster 2016). Acoustic cues are often favoured for that purpose since they can travel far and across obstacles, and may be easier to use in a crowd than e.g. olfactory cues (often requiring direct contact; Tibbetts & Dale 2007). Across species, cues to caller identity can be coded in various spectral, temporal, and amplitude features, and carried by both stereotyped and variable vocalisations (see review in Wyman et al. 2022).

Yet vocalisations do not exclusively carry information on identity, but may instead inform on multiple aspects of the sender, such as their sex (e.g. Cordeiro et al. 2012, Volodin et al. 2016), size (e.g. Briefer & McElligott 2011a, Wyman et al. 2012), or physiological state (e.g. Yoshihara & Oya 2021, Briefer et al. 2022). This creates a potential limitation to identity coding – one can expect that this information may in some cases be overridden by other, more urgent information, in cases where different types of information are not segregated in different, at least partially independent parameters ("segregation of information"; Marler 1960). In particular, some parameters of vertebrate vocalisations tend to be reliable indicators of the caller's affective state (Briefer 2020). For instance, situations of a negative valence and/or high arousal often result in longer duration and higher frequencies, and an increased entropy and presence of non-linear phenomena in the uttered vocalisations (Briefer 2020, Gavojdian et al. 2024), which in some cases might lead to reduced vocal individuality (e.g. Rendall et al. 1999, Green et al. 2019, Osiecka et al. 2024).

Vocalisation have been shown to vary in how individualised there are depending on their function ("social function hypothesis"; Snowdon et al. 1997). For instance, vocalisations aimed at specific individuals within the group are predicted to be more individualised than those aimed at the whole group (Lemasson & Hausberger 2011). Typically, this results in affiliative calls (e.g. contact or mating calls) aimed at specific individuals showing higher individuality, while agonistic and particularly alarm calls aimed at the whole group are more stereotyped (Lemasson & Hausberger 2011; Linn et al. 2021). Low individuality in calls indicating higher urgency might, at the same time, benefit the sender by inducing confusion and increasing chances that any receivers in the surrounding might come and help, as it is the case in offspring distress calls (Lingle et al. 2012). A pattern hence seems to emerge where more emotionally positive vocalisations – often produced in one to one affiliative contexts - could be more individualised, while those produced during negative contexts could show less individuality. In addition, this

pattern might not be limited to differences between acoustically distinct call categories, but

could also occur within specific call types (e.g. contact calls), which can be produced in both

positive and negative contexts (such as horse whinnies, Briefer et al 2015, or pig grunts, Briefer

et al. 2019).

Most ungulate species, including these commonly bred as livestock, naturally live in socially

complex and often cohesive groups (Szemán et al. 2021), and exhibit prosocial behaviours such

as e.g. allogrooming (Hodgson et al. 2024). Not surprisingly, they are often vocally active

animals, coding (e.g. Favaro et al. 2014, Briefer et al. 2015, Maigrot et al. 2019, Briefer et al.

2022, Laliotis et al. 2023), and perceiving (e.g. Lingle & Riede 2014, Briefer et al. 2017,

Baciadonna et al. 2019) important social information in their calls. Here, we tested if

individuality is maintained in negative compared to positive contact calls of seven ungulate

species: cattle (*Bos taurus*), goats (*Capra hircus*), sheep (*Ovis aries*), domestic pigs (*Sus scrofa*

domestica), wild boars (*Sus scrofa*), horses (*Equus caballus*), and Przewalski's horses (*Equus*

ferus przewalskii). All these species show some similarities in vocal expression of emotions

(Lefèvre et al. in rev), and most of them have been shown to produce individually specific calls

(e.g. Lemasson et al. 2009, Briefer & McElligott 2011b, Padilla de la Torre et al. 2016, Syrová

et al. 2017, Sèbe et al. 2018). However, except for cattle in which individuality was shown to

be present in calls emitted in both negative and positive valence (Green et al. 2019), we do not

know yet know how these two types of information interfere, and if individuality is favoured

under a specific emotional valence across species.

This study explores (1) the efficiency of contact calls' classification to caller within and across

the valenced contexts, (2) the retention of individual information content across contexts, and

(3) the acoustic parameters responsible for identity coding across these contexts. We predicted,

based on the social function hypothesis, that contact calls will retain some individual signatures

across emotional contexts, but that these emitted in negative contexts would should lower

individuality due to their often more chaotic structure and their function in addressing less

specific individuals.

Methods

Dataset

This study revisits the data from Lefèvre et al. (in rev), which integrates recordings from Padilla
de la Torre et al. 2015, Briefer, Tettamanti & McElligott 2015, Briefer et al. 2015, 2019,
Maigrot et al. 2017, 2018 & Lefèvre et al. in prep. This dataset consists of 3181 contact calls
emitted by seven ungulate species (cows, goats, sheep, pigs, wild boars, horses and Przewalski's
horses) by known, adult individuals. Calls were recorded in known contexts assigned to a
putatively negative or positive valence based on the context of production (i.e., corresponding
to fitness threatening/frustrating vs beneficial/relieving situations – such as isolation vs reunion;
see e.g. Paul & Mendl 2018, Kremer et al. 2020), and validated based on behavioural as well
as physiological (for domestic species) indicators of emotions in previous studies (see the
details on behavioural contexts and corresponding references to individual studies in
Supplementary Material X (from Lefèvre et al in rev), and details on recording procedures in
the individual studies (Padilla de la Torre et al. 2015, Briefer, Tettamanti & McElligott 2015,
Briefer et al. 2015, 2019, Maigrot et al. 2017, 2018 & Lefèvre et al. in prep). To avoid pseudo
replication, each of the calls for any given individual comes from an independent sequence.

Acoustics analysis

All analyses were performed in R environment (v. 4.1.3). All calls were automatically analysed
using the *analyze* function of *soundgen* package (Anikin 2019). Only median values of relevant
parameters with no missing entries were kept for their robustness against outliers and skewed
data distributions. Individuals with at least five entries were kept for further analysis (see Table
2, Results, and more details in Lefèvre et al in rev).

Principal components analysis

First, we confirmed that the data were suitable for factor analysis, using the Kaiser-Meyer-
Olkin criterion (*KMO* function, *EFAtools* package; Supplementary Material 1). We then ran a
principal components analysis (PCA) on all calls of each species separately (*prcomp* fuction,
stats package; Supplementary Material 2).

Classification to individuals

For each species and valence, individuals with at least five extracted calls were identified.
Among these, five calls per individual were randomly selected for further analysis. Those
randomly selected calls were then used in a discriminant function analysis (DFA) with leave-
one-out cross-validation. This was performed separately for each species, for (1) all calls pooled
together, (2) calls associated with a negative valence, and (3) calls associated with a positive

valence, using the *lda* function of the *MASS* package (Ripley et al. 2023), with the individuals ID as a test factor, and the PC scores with eigenvalues > 1 (Supplementary Material 2) as variables. Significance of each model was calculated using the Fisher test (*fisher.test* function, *stats* package).

Since support vector machine (SVM) classifiers can be more reliable than linear methods (such as DFA) in individuality studies, particularly for unbalanced datasets such as this one (see Arnaud *et al.* 2023), we have also performed the following procedures separately for each species. First, data dimensions of the raw acoustic variables were reduced using supervised uniform manifold approximation and projections (S-UMAP; *umap* function, *uwot* package), with number of neighbours = 30, metric = euclidean, minimum distance = 0.01. The obtained two-dimensional coordinates were then used as input for the SVMs. The data were subset into 80:20 training and test datasets, and a classification task built for each subset (*makeClassifTask* function, *mlr* package, with the animals' ID as target). A learner was then created (*makeLearner* function, *mlr* package) and corrected for individual weights (*makeWeightedClassesWrapper* function, *mlr* package). This weighted learner was then trained (*train* function, *mlr* package) on the training task, and used to classify the test task (*predict* function, *mlr* package). SVM classification accuracy was extracted using the *performance* function (*mlr* package). This was performed for each valence separately, as well as for all calls pooled together.

Information content

To investigate whether the individual information content of the calls varies between affective valence of the caller, we used Beecher's information statistic, Hs (Beecher 1989) – a robust, standard method to calculate bits of information carried by a signal and assess the approximate number of individuals that can be theoretically distinguished based on this signal (Linhart *et al.* 2019).

All previously obtained principal components (PC1-11) were used to calculate the Hs, using the *calcHS* function (*IDmeasurer* package). Hs was calculated for each valence separately. To test whether the putative valence results in a change in Hs, we ran a linear mixed model with species as a random effect (*lmer* function, *lme4* package). Model assumptions were checked using the *simulateResiduals* function of the *DHARMa* package, based on the fitted model. To obtain p-values and significance of the LMMs, we used the *Pbmodcomp* function (*pbkrtest* package; using the PBtest output), and Bonferroni adjustment to correct for multiple testing (i.e., the p-values retained significance at 0.005).

 Parameters coding individuality

To understand which raw acoustic parameters carry information about the caller's identity in
different contexts, we calculated the potential of individuality coding (PIC; Robisson *et al.*
1993) for each of the 11 parameters (Table 1), using the *calcPIC* function (*IDmeasurer*
package). This was done for each species, separately for the positive and negative valence. The
obtained values were then input in linear mixed models (LMMs), with the PIC value of each
parameter as the response variable, valence as fixed factor of interest, and species as a random
control factor (*lmer* function, *lme4* package). Model assumptions and p values were computed
as mentioned above (*Information content*).

Results

Classification to individuals

In all species, except for *B. taurus, E. ferus przewalskii* and *S. scrofa*, calls could be correctly
classified to individuals above chance levels across valenced states by the DFA, and for most
species, except for *O. aries* and *E. Caballus*, the DFA relative cross-classification level (i.e.,
the ratio of correct to chance classification levels) was slightly higher in positive contexts (Table
1, Figure 1). Accordingly, for *B. taurus, E. ferus przewalskii* and *S. scrofa*, positive, but not
negative calls, were classified to the correct individuals above chance levels by the DFA (Table
1, Figure 1). In addition, in all species, but *O. aries* and *S. scrofa*, SVM performance % were
higher in positive than negative valence (Table 1, Figure 2). Note that SVMs and the DFA gave
rather different results, with SVMs having a much better performance for some species (Table
1).

Table 1. Results of the DFA and SVM performance. In most, but not all cases, calls could be correctly assigned to the individual above chance levels across valence, even though the percentage of correct classification may be low.

Family	Species	Context	SVM performance %	DFA: Correctly cross-classified %	DFA: Chance level %	p-value	DFA: Relative cross-classification level
Bovidae	*B.taurus*	-	10.3	7.86	3.57	0.37	2.2
		+	41.67	64.00	20.00	**<0.001*****	3.2
		all	NA	8.28	3.45	0.213	2.4
	C. hircus	-	63.46	68.18	41.74	**<0.001*****	1.6
		+	77.78	80.00	33.33	**<0.001*****	2.4
		all	NA	52.17	27.41	**<0.001*****	1.9
	O.aries	-	25.37	41.00	5.00	**<0.001*****	8.2
		+	12.5	80.00	50.00	**<0.001*****	1.6
		all	NA	33.64	4.55	**<0.001*****	7.4
Equidae	*E.caballus*	-	16.67	53.33	8.33	**<0.001*****	6.4
		+	34.15	32.5	12.5	**0.001*****	2.6
		all	NA	30.00	7.14	**<0.001*****	4.2
	E.ferus przewalskii	-	62.5	32.00	20.00	0.076	1.6
		+	66.67	100.00	50.00	**<0.001*****	2.0
		all	NA	36.67	16.67	**0.002****	2.2
Suidae	*S.scrofa*	-	3.23	14.12	5.88	0.090	2.4
		+	9.52	30.00	10.00	**<0.001*****	3.0
		all	-	18.82	5.88	**0.009***	3.2
	S.scrofa domestica	-	6.45	11.72	3.45	**0.029***	3.4
		+	4.08	15.56	3.70	**0.008***	4.2
		all	NA	10.67	3.33	**0.049***	3.2

-/+/all indicate calls of putatively negative or positive valence, and all calls pooled together. * indicates statistical significance

Category   Negative   Positive   All

Figure 1. Relative cross-classification levels (from the discriminant function analysis) show
the strength of classification to individual (i.e., the ratio of correct to chance classification
levels) across emotional valence and species. Animal silhouettes obtained from PhyloPic.

Figure 2. S-UMAP classification to individual shows the calls' distribution in the acoustic
space. Clustering efficiency varies across species and affective contexts. Percent values indicate
the classification accuracy of the SVMs. Animal silhouettes obtained from PhyloPic.

Information content

We observed no pattern in Hs changes between valenced states across the studied species
(LMM: p-value = 0.61). Hs values changed between valence in some – but not all - species
(Fig. 3). Except for the two horse species, where the information content was higher in the
negative contexts, this was not consistent in other related species (Figure 3).

Figure 3. Hs as a function of valence. Boxplots represent all species pooled together, and
symbols the discreet values for each of the study species. There were no patterns of information
content change in calls of positive and negative valence across the studied species.

Parameters coding individuality

None of the acoustic parameters showed significant differences in PIC values across positive

and negative valence (LMM, Table 2). For each species, one parameter seemed to remain a

particularly stable indicator of identity between valence: in all cases, except of the *Suidae,* this

was the 75th quantile of the frequency spectrum (Table 2). For *S. scrofa domestica*, this

parameter was Weiner Entropy, while for *S. scrofa*, it was the Duration instead.

Table 2. Potential for identity coding (PIC) for the 11 raw acoustic parameters. After Bonferroni adjustments, PIC values showed no differences

between the positive and negative contexts.

	Bovidae						Equidae				Suidae				
	B.taurus		C. hircus		O.aries		E. caballus		E.ferus przewalskii		S.scrofa		S.scrofa domestica		
Parameter	+	-	+	-	+	-	+	-	+	-	+	-	+	-	p-value
Duration (s)	1.35	1.10	1.78	**1.67**	1.68	1.43	**1.46**	**1.92**	1.23	1.03	1.39	1.25	**1.54**	**1.58**	0.505
Amplitude Envelope Frequency (Hz)	1.23	0.92	0.95	1.22	**2.22**	**1.81**	1.25	1.04	1.10	**1.49**	**1.43**	1.15	1.16	NaN	0.579
Amplitude	**1.53**	1.10	1.18	1.12	1.47	1.21	**1.69**	1.08	1.14	1.07	1.09	1.05	1.19	1.12	0.050
Weiner Entropy	1.27	**1.30**	1.92	1.48	2.00	1.40	**1.51**	1.20	1.08	**1.20**	**1.44**	**1.34**	**1.36**	1.30	0.098
Peak Frequency (Hz)	**1.42**	1.17	1.99	**1.79**	**2.37**	1.45	1.13	**1.34**	1.26	1.10	**1.90**	**1.26**	1.24	1.11	0.084
Q25% (Hz)	1.32	1.07	**2.21**	1.57	2.05	1.46	1.03	**1.34**	**1.48**	1.13	1.44	**1.37**	**1.55**	**1.27**	0.072
Q50% (Hz)	**1.67**	1.14	**2.13**	**1.83**	1.68	1.55	1.27	1.21	**1.85**	1.08	**1.58**	1.18	1.25	**1.55**	0.100
Q75% (Hz)	**1.97**	**1.27**	**2.64**	**1.62**	**2.20**	**2.22**	**1.47**	**1.34**	**1.83**	**1.26**	1.41	**1.26**	1.24	1.17	0.047
Roughness	1.36	**1.27**	1.44	1.27	1.96	**1.56**	1.41	**1.30**	1.02	1.03	1.31	1.11	1.07	1.08	0.043
Spectral Centroid (Hz)	**1.53**	**1.24**	2.07	1.53	**2.57**	**1.72**	1.29	**1.34**	**1.85**	1.16	1.42	**1.33**	1.23	1.17	0.042
Spectral Slope (dB/kHz)	1.08	**1.35**	**2.18**	1.58	1.36	1.51	1.30	**1.27**	**1.40**	**1.40**	1.40	1.21	**1.35**	**1.36**	0.600
All values except duration are medians. +/- indicate valence. Bold indicates the four highest scores in each valence for the species. P-values obtained from PBtest. After Bonferroni adjustment, p-values retain significance at 0.005.															

Discussion

We investigated the individuality in vocalisations uttered in putatively positive and negative
contexts in seven ungulate species. Call classification to the correct individuals could be
efficiently performed in most, but not all species across valence, with slightly higher
performances for positive than negative calls in all but two species, and large variation between
methods (DFA or SVM). There were no cross-species patterns in the retention of individual
information content (Hs) across contexts. In each species, one acoustic parameter seemed to
have a particularly stable potential of identity coding (PIC) across valenced states (Q75% for
all but *Suidae*).

We predicted that the identity information might decrease in negative contexts. This prediction
was based on the *arousal* and *function* of the calls. As negative vocalisations, which are often
of higher *arousal* than positive vocalisations, can be more chaotic, their information content
may indeed drop (Osiecka et al. 2024), overridden e.g. by information about the level of stress
experienced by the vocalising animal (Corvin et al. 2024) - yet this is not always the case
(Probert et al. 2023), particularly when positive vocalisations reflect high arousal as well (e.g.
excitement). This may instead depend on the social *function* of these calls (Snowdon et al.
1997), i.e. whether the calling animal expects the members of their social group to react (and
thus needs to convey information on their identity), expects anyone to react (and thus needs to
convey urgency rather than identity), or simply vocalises in an uncontrolled manner (again
reflecting the urgency or arousal). Indeed, isolation calls often retain individuality (e.g. Symmes
et al. 1979, Scheumann et al. 2012, Green et al. 2019), while calls intended to elicit release
and/or produced in situations of high arousal tend to lose this information (e.g. Reers & Jacot
2011, Keenan et al. 2020, Corvin et al. 2024, Osiecka et al. 2024). In other words, when a
situation requires a reaction from a specific known individual, and thus recognition by them, it
might be beneficial to keep the individual information content of the calls high, whether the call
reflects a negative or positive emotion (Lingle et al. 2012, Wyman et al. 2022).

In our case, all analysed calls were contact calls (also referred to as "attraction" or "isolation"
calls in the literature; see Lingle et al. 2012) –used to maintain social cohesion. The fact that
calls of all species except domestic cattle, Przewalski's horses and wild boars could be correctly
classified to the caller above chance level within and across emotional contexts indicates that a
particularly strong identity coding is in place. In the case of Przewalski's horses, this identity
loss indicated by the discriminant function analysis is likely an artifact of the small number of

individuals sampled: both support vector machine (SVM) and Hs showed high, or even elevated
individuality of their calls.

Interestingly, previous studies have shown that different domestic cattle call types retain
individuality over putatively negative and positive contexts (i.e. during social isolation vs.
anticipation of feed; Green et al. 2019, Gavojdian et al. 2024). Here, mother-calf separation
resulted in a decreased identity, measured both by classification efficiency and information
content. While we are not sure why this might be, arousal (which we did not account for in this
study) could play a role. Additional studies including robust physiological measures would be
needed to better understand this discrepancy.

Interestingly, the individual information content (as measured by Beecher's statistic; Hs) in the
calls of both domestic and feral horses, as well as sheep, was significantly higher in negative
than positive contexts. This makes sense in case of visual isolation from the herd: if vocal cues
are all there are, calls may need to indicate the caller's identity particularly well. On the other
hand, the calls of cattle, goats, and wild boars showed a reduced Hs in negative contexts.
Overall, the interplay between emotional states and identity coding seemed to be more species-
than context-specific. We did not see the same patterns in closely related species, and the
number of sampled species was too low to run a phylogenetic analysis. However, we encourage
others to publish cross-species comparable indices, such as Hs (Beecher 1989, Linhart et al.
2019) to enable such comparisons in the future.

Practical implications

The fact that in most species the individuals could be identified based on sound across
emotional states is promising for developing targeted welfare monitoring systems, e.g.
precision livestock farming. Our results also indicate that, where one intends to monitor and
recognise known individuals, it might be crucial to include model corrections for emotional
valence in order to maintain efficient recognition. For example, acoustic capture-recapture is
slowly implemented in automated population monitoring of some species (e.g. Terry et al. 2005,
Laiolo et al. 2007, Longden et al. 2020). A baseline understanding of affective expression and
its impact on vocal individuality in the monitored species would improve such population
counts.

From the perspective of studying vocal individuality, correcting for affective states – or
including calls emitted in various states, including positive and negative context, as well as high

and low arousal – would be advisable to avoid under- or over-estimation of the commonly used
individuality indices (see Linhart et al. 2019).

Caveats and issues

The dataset is heavily imbalanced in terms of sample sizes for different species and individuals.
Unfortunately, the data structure did not allow us to run meaningful permuted discriminant
function analysis (Mundry & Sommer 2007), which would have been the preferred method
here. To correct for this imbalance, we have run the DFA on a sample size limited down to 5
calls per individual. While this eliminates the issue of over/under-representation, it also heavily
limits the dataset available for the linear analysis. The machine learning methods may be much
more reliable here, since they include the correction for individual weights within the learners,
without unnecessarily limiting the available data. Therefore, we suggest to consider the SVM
performance as the more reliable indicator of vocal individuality.

This said, we used the best common settings for S-UMAPs and SVMs for all species – note
however, that the classifier performance could be improved by fine-tuning separate models for
each of the species. We have decided to use shared settings for the sake of simplicity, but also
meaningful comparisons. However, for practical use, such as automated acoustic detectors for
conservation and individual-based counting methods (e.g. Terry et al. 2005, Laiolo et al. 2007,
Longden et al. 2020), or welfare and precision livestock farming (e.g. Schön et al. 2004,
Mcloughlin et al. 2019, Herborn et al. 2020, Gavojdian et al. 2024), species-specific fine-tuning
is absolutely necessary to maximise the detectors' performance.

Finally, the actual efficiency of vocal recognition by the animals likely differs from both the
optimised machine learning methods and the generalised results of this study. In the end, the
real-life recognition can only be tested using playback experiments, i.e. asking the animals to
distinguish between the calls of familiar vs nonfamiliar animals in different emotional contexts
(e.g. Briefer et al. 2017), and likely to differ not only between the state of the caller, but also
the receiver. We suggest that such experiments might help us understand the emotional impacts
on individual recognition in the future.

Conclusions

Our results indicate a nuanced interplay between emotional expression and vocal individuality,
and suggests that species-specific strategies rather than cross-species trends exist, likely

corresponding to their social structures. This highlights the importance of correcting for

emotional valence in studies and practical applications of vocal individuality.

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Ethics statement

All acoustic recordings were collected in accordance with the current laws of the UK (goats) and Switzerland (other species), and approved by ethical committees as part of our previous studies. The experiments carried out to collect the goat recordings were reviewed by the U.K. Government Home Office inspector for Queen Mary, University of London. For the other species, experiments were approved by the Swiss Cantonal authorities (approval numbers: pigs, TG02/2014; wild boars and Przewalski's horses, ZH011/15; sheep, ZH233/18; horses, VD2689; cattle, ZH49/2014).

Authors' contributions:

ANO: Conceptualization, Methodology, Formal analysis, Writing – Original Draft, Writing – Review & Editing, Visualisation; RL: Conceptualization, Methodology, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing; EFB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – Original Draft, Writing – Review & Editing, Supervision.

Competing interests

Authors declare no competing interests.

Data availability statement

Raw data and the full code generated in this study are available at:

https://osf.io/fm92j/?view_only=1297922ef1864ada87de5528d047243e