Measuring individual identity information in animal signals: Overview and performance of available identity metrics

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Abstract

1. Identity signals have been studied for over 50 years but, and somewhat remarkably, there is no consensus as to how to quantify individuality in animal signals. While there are a variety of different metrics to quantify individuality, these methods remain un-validated and the relationships between them unclear.
2. We contrasted three univariate and four multivariate identity metrics (and their different computational variants) and evaluated their performance on simulated and empirical datasets.
3. Of the metrics examined, Beecher's information statistic (H_S) performed closest to theoretical expectations and requirements for an ideal identity metric. It could be also easily and reliably converted into the commonly used discrimination score (and vice versa). Although Beecher's information statistic is not entirely independent of study sampling, this problem can be considerably lessened by reducing the number of parameters or by increasing the number of individuals in the analysis.
4. Because it is easily calculated, has superior performance, can be used to quantify identity information in single variable or in a complete signal and because it indicates the number of individuals that can be discriminated given a set of measurements, we recommend that individuality should be quantified using Beecher's information statistic in future studies. Consistent use of Beecher's information statistic could enable meaningful comparisons and integration of results across different studies of individual identity signals.

Keywords: Individual recognition, Social behavior, Identity signal, Beecher's Information Statistic, Acoustic identification, Acoustic discrimination, Vocal individuality, Discriminant analysis

Introduction

The fact that individuals differ in consistent ways is a both a central attribute of life and one that underlies a number of theoretically important questions such as explaining cooperative behavior or understanding the evolution of sociality (Crowley et al., 1996; Bradbury & Vehrencamp, 1998; Tibbetts, 2004). Such individuality can also be important in wildlife conservation as well when it is used to help census or monitor individuals based on individually-distinctive traits (Terry & McGregor, 2002; Blumstein et al., 2011). And, because, animals may base their decisions on the identity of the individual with whom they interact or respond to (Wilkinson, 1984; Godard, 1991), there may be selection to both produce individually-distinctive signals, and selection to discriminate among them (Tibbetts & Dale, 2007; Wiley, 2013).

Quantification of individual identity (individuality) requires the assessment of variation in one or more traits between at least two individuals. For identity signals to function properly, they should maximize the between-individual variation and minimize the within-individual variation (Beecher, 1982, 1989). A variety of identity metrics have proliferated because of recognized biases (e.g., it is more likely to find similar individuals in larger populations and, hence, it will be more difficult to discriminate individuals in large populations or studies involving more individuals). These biases make the comparison of results among studies unreliable (Beecher, 1989; Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010). Additionally, some existing metrics were considered unsuitable for a particular signal type (Searby & Jouventin, 2004). Nevertheless, new alternatives were not always thoroughly tested and were not shown to be superior to the metrics they attempted to replace. Furthermore, there are methodological problems that result from the calculation of particular identity metrics, and some studies have used different equations to calculate the same identity metric. Thus, somewhat remarkably given its importance, there is no consensus about how to properly measure identity. As a result, researchers have generally avoided quantitative comparisons between studies (Insley, Phillips, & Charrier, 2003). In a few cases, researchers tried to overcome problems with identity metrics in comparative analyses by using exactly the same methods

77 across involved species (Beecher, Medvin, Stoddard, & Loesche, 1986; Lengagne, Lauga, & Jouventin,
78 1997; Pollard & Blumstein, 2011). Thus, hundreds of isolated studies have been published on
79 individuality in animal signals but because they used different metrics there is limited prospect that
80 we can benefit from the cumulative evidence of these studies. The lack of a commonly used identity
81 metric is a major impediment toward understanding the evolution of identity signaling and indeed,
82 the evolution of individuality.

83 Here, we review previously developed univariate (quantifying individuality within a single trait)
84 and multivariate metrics (quantifying individuality across multiple traits) that have been used to
85 quantify individual identity information in signals and we test their performance on simulated and
86 empirical datasets. In particular, we examine the following metrics: F-value, Potential of individual
87 coding PIC, Beecher's information statistic H_S, Information capacity H_M, and Mutual information MI.
88 We further evaluate different computational variants found in the literature in case of PIC and H_S
89 (see Table 1 and Supplement 1 for a detailed overview of metrics and their variants).

90 Table 1. Overview of the identity metrics and their variants

Metric variant and equation	description	reference	IDmeasurer function
$F = \frac{MS_b}{MS_w}$	F from one-way ANOVA where the individual is treated as independent variable and trait as dependent variable; MS_b = between group mean squares; MS_w = within group mean squares; calcF	e.g., Miller, 1978	calcF
$PIC_{betweentot} = \frac{CV_{betweentot}}{CV_W}$	$CV_{betweentot}$ = between individual coefficient of varaiation calculated from all data points; CV_w = within individual coefficient of variation	e.g., Robisson, Aubin, & Bremond, 1993	calcPICbetweentot
$PIC_{betweenmeans} = \frac{CV_{betweenmeans}}{CV_W}$	$CV_{betweenmeans}$ = between individual coefficient of variation calculated with means from each individual; CV_w = within individual coefficient of variation	e.g., Lein, 2008	calcPICbetweenmeans
$H_{Sntot} = log_2\sqrt{\frac{F + n_{tot} - 1}{n_{tot}}}$	F = ANOVA F-value; n_{tot} = total sample size	possible variant from Beecher, 1989	calcHSntot
$H_{Sngroups} = log_2\sqrt{\frac{F + n_{groups} - 1}{n_{groups}}}$	F = ANOVA F-value; n_{groups} = number of groups (individuals)	possible variant from Beecher, 1989; e.g., Pollard, Blumstein, & Griffin, 2010	calcHSngroups
$H_{Snpergroup} = log_2\sqrt{\frac{F + n_{pergroup} - 1}{n_{pergroup}}}$	F = ANOVA F-value; $n_{pergroup}$ = number of samples in each group (observations per individual)	possible variant from Beecher, 1989	calcHSnpergroup
$H_{Svarcomp} = log_2\frac{\sigma_T}{\sigma_W}$	σ_T = total variance in mixed model; σ_W = residual variance associated with random factor in mixed model	Beecher, 1989; Carter, Logsdon, Arnold, Menchaca, & Medellin, 2012	calcHSvarcomp
$H_{Snpergroup} = log_2\sqrt{\frac{F + n_{pergroup} - 1}{n_{pergroup}}}$	F = ANOVA F-value; $n_{pergroup}$ = number of samples in each group (observations per individual); original variables are subjected to PCA to get uncorrelated components and H_S is calculated and summed over each independent component	Beecher, 1989	calcHSnpergroup
$H_M = log_2\sqrt{\frac{F_M + n - 1}{n}}$ $F_M = \frac{n-1}{g-1} * \frac{dist_t - g * dist_w}{dist_w}$	$dist_t$ = sum of distances of all samples from their centroid; $dist_w$ = sum of distances of samples within individual to its centroid; n = number of observations; g = number of groups;	Searby & Jouventin, 2004	calcHM
$DS = \frac{C}{N}$	C = samples correctly classified by Discriminant analysis; N = total number of samples	e.g., Hafner et al., 1979	calcDS
$MI = \sum_{i,j} log_2\frac{p(i,j)}{p(i) * p(j)}$	p(i) = probability of predicted individual; p(j) = probability of actual individual; p(i,j) = probability of match between predicted and actual individual	Mathevon et al., 2010	calcMI

91

We compare the performance of metrics to hypothetical ideal identity information metric. The main principle of measuring individual identity in continuous traits is to quantify the ratio of between and within individual variation (Beecher, 1982, 1989; Robisson, Aubin, & Bremond, 1993; Searby & Jouventin, 2004). Thus, an ideal individual identity metric should be expressed on a ratio scale with a meaningful zero value, equivalent to the situation when there is no between individual variation. Further, there is no expected upper limit for individuality. High between to within individual variation ratio indicates easy discrimination of individuals.

The datasets for the assessment of individual identity in different species vary in properties such as the number of individuals, the number of samples per individual, the number of variables measured (i.e., number of individualistic traits) and the covariance between the multiple variables measured. Hence, we further propose that an ideal identity metric should be robust or respond predictably to these dataset parameters to allow meaningful comparisons between studies. Therefore, an ideal identity metric: 1) should not be systematically biased by the sampling effort, i.e., there should be no systematic effects of number of individuals and number of calls per individual in a study on individuality estimate, and the sampling should ideally only impact on precision of individuality estimate; and 2) in the multivariate case, it should well capture the intrinsic multidimensionality of identity signals. In particular, it should rise with number of meaningful variables because each of the uncorrelated variables can encode another level of individual variation. In addition, it should also decrease with covariance between the variables because increasing covariance between variables essentially decreases the number of independent variables. For our comparison we gave the same weight to all criteria because these are very basic requirements and an ideal metric should fulfill all of them. In addition, we will list other potential pros and cons of each metric to provide a comprehensive evaluation of existing metrics.

We also wished to see if each of two commonly used metrics (Beecher's information statistic H_S, and discrimination score DS) could be converted to the other metric. We focused on H_S and DS

metrics only. DS has been used in the vast majority of past studies and DS has been found to correlate well with potentially unbiased H_S in a previous study (Beecher, 1989). However, the previous study only tested the relationship between H_S and DS on datasets with equal number of individuals and observations per individual, thus, ignoring the known biases associated with DS. Reliable conversion of DS into potentially unbiased H_S could facilitate comparative analyses of results reported in past and future studies.

Material and methods

We used R for simulations and statistical analysis (R Core Team, 2012). Functions to calculate identity metrics, associated functions and datasets are available within an IDmeasurer package. This package is available on CRAN (https://cran.r-project.org/web/packages/IDmeasurer/index.html) and GitHub (https://github.com/pygmy83/IDmeasurer).

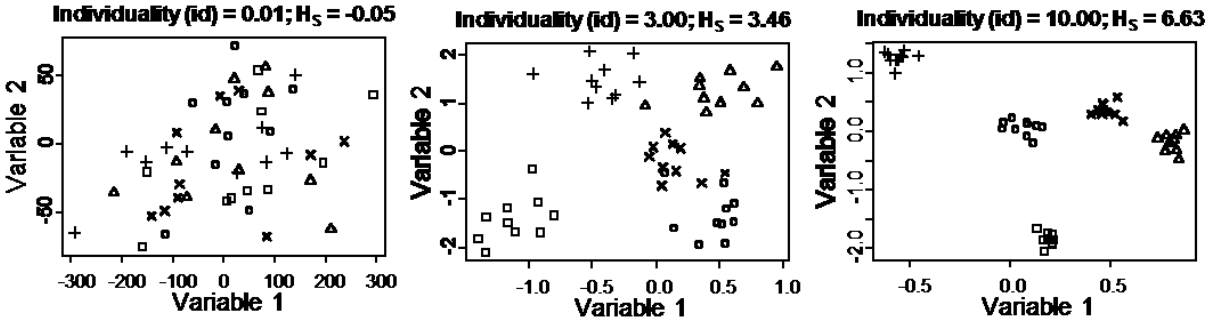
Datasets

Simulated datasets. Datasets were constructed to mimic typical data on individuality. Parameters of datasets vary among studies. In particular, there are different numbers of individuals, observations (samples) per individual, variables, and different covariances among variables. Effect of these parameters was simulated along with individuality within datasets. The level of individual identity in data was modified by changing the ratio of between and within individual variance in accordance with theoretical assumptions of individual identity signals and previous studies (Beecher, 1989; Searby & Jouventin, 2004). We developed R scripts involving “rnorm” and MASS package (Venables & Ripley, 2002) “mvrnorm” function to generate the datasets. These functions generate random values with a given standard deviation around pre-specified mean and, in “mvrnorm”, with pre-specified covariance.

We constructed datasets with univariate and multivariate normal distributions with parameters covering a wide range of values, specifically, five values for individuality (id = 0.01, 1, 2.5, 5, 10), five values for number of observations per individual (o = 4, 8, 12, 16, 20), eight values for number of individuals (i = 5, 10, 15, 20, 25, 30, 35, 40). Additionally, for multivariate datasets, five values for

covariance among variables (cov = 0, 0.25, 0.5, 0.75, 1) and five values for number of variables (p = 2, 4, 6, 8, 10). Thus, 200 and 5000 unique parameter combinations were possible in case of univariate and multivariate datasets respectively. Individuality (id) represents the ratio of standard deviations between and within individuals (id = $SD_{between}$ / SD_{within}; $SD_{between}$ was calculated from means for each individual and SD_{within} was set to be $SD_{between}$ / id) (Fig. 1). A single covariance (cov) value was used in the variance-covariance matrix to define covariances between all pairs of variables. For univariate datasets, we first generated individual means for a predefined number of individuals "i" (normal distribution, "rnorm" function, mean = 1000, $SD_{between}$ = 1) and then we generated a predefined number of random observations "o" around each individual mean (normal distribution, "rnorm" function, mean = individual mean, SD_{within} = $SD_{between}$ / individuality "id"). In the multivariate case, we first created a matrix representing mean individual values of variables for each of the individuals (multivariate normal distribution, "mvrnorm" function, mean for each variable = 0, variance-covariance matrix). Variances on the diagonal of the covariance matrix were set equal to 1 (hence $SD_{between}$ = 1) and all covariances between variable pairs were set equal to the predefined covariance "cov". Then, we generated a predefined number of random observations "o" around each individual and a variable mean ("rnorm" function, mean = individual mean, SD_{within} = $SD_{between}$ / individuality "id").

We asked how dataset parameters (i, o, p, cov, id) influenced the value of each identity metric. To explore this, 20 randomization cycles were run for each unique combination of parameter values. For example, in the multivariate case, 20 * 5000 = 100 000 independent datasets were generated (datasets 1-20: i = 5, o = 4, p = 2, cov = 0, id = 0.01; datasets 21-40: i = 10, o = 4, p = 2, cov = 0, id = 0.01; … ; datasets 99 981-100 000: i = 40, o = 20, p = 10, cov = 1, id = 10). Identity metrics were calculated for each dataset.



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167 **Figure 1**. Illustration of three artificial multivariate datasets that differ only in the individuality used
168 to generate datasets. Settings for the function generating these datasets: i = 5, o = 10, p = 2, cov = 0,
169 id = 0.01, 3, and 10.

170 **Empirical datasets.** While the general performance of identity metrics was evaluated on simulated
171 datasets, empirical datasets were used to evaluate the consistency of DS and H_S metrics and
172 reliability of H_S and DS conversion on real data. We used six empirical datasets from four different
173 species: little owls *Athene noctua* (ANmodulation, ANspec) (Linhart & Šálek, 2017), corncrake *Crex*
174 *crex* (CCformants, CCspec) (Budka & Osiejuk, 2013), yellow-breasted boubous *Laniarius atroflavus*
175 (LAhighweewoo) (Osiejuk et al. unpublished data), and domestic pigs *Sus scrofa* (SSgrunts) (Syrová,
176 Policht, Linhart, & Špinka, 2017) (Figure 2). In two species – corncrakes and little owls – calls were
177 described by two different sets of variables. In little owls, we described calls by frequency
178 modulation by measuring fundamental frequency at 10 measuring points evenly spread through the
179 duration of the call (ANmodulation) or parameters describing the distribution of the frequency
180 spectrum such as peak frequency, minimum and maximum frequencies and frequencies dividing
181 spectrum by energy content (ANspec). In corncrakes, we used formants (CCformants) and
182 parameters describing the distribution of the frequency spectrum (CCspec) (see the Supplement 2 for
183 detail description of empirical datasets). Because datasets varied with respect to the number of
184 individuals (33 – 100) and the number of calls per individual available (10 – 20), we scaled all datasets
185 down to lowest common denominator by randomly selecting individuals and calls from bigger
186 datasets. Eventually, each dataset had 33 individuals and 10 calls per individual. Each dataset also

used different numbers of variables to describe the calls' acoustic structure (ANmodulation = 11, ANspec = 7, CCformants = 4, CCspec = 7, LAhighweewoo = 7, SSgrunts = 10). In all these empirical datasets, assumptions of multivariate normality were tested (Korkmaz, Goksuluk, & Zararsiz, 2014), but not met. We found various issues on the level of univariate variables and the whole dataset. For instance, there were issues with outliers, skewness, kurtosis, and multimodal distributions (see Supplement 2 for univariate histograms and multivariate Chi-square Q-Q plot). Normality issues are common for research studies on acoustic individual identity. Authors deal with normality issues by eliminating problematic variables (e.g., Couchoux & Dabelsteen, 2015), using non-parametric classification methods (e.g., Mielke & Zuberbuehler, 2013), or by relying on robustness of cross-validated DFA and PCA towards relaxed assumptions (e.g., Mathevon et al., 2010). We used the last approach. If the assumptions of discriminant analysis are not met the results should be less stable when using different sampling and hence our results should be viewed as conservative.

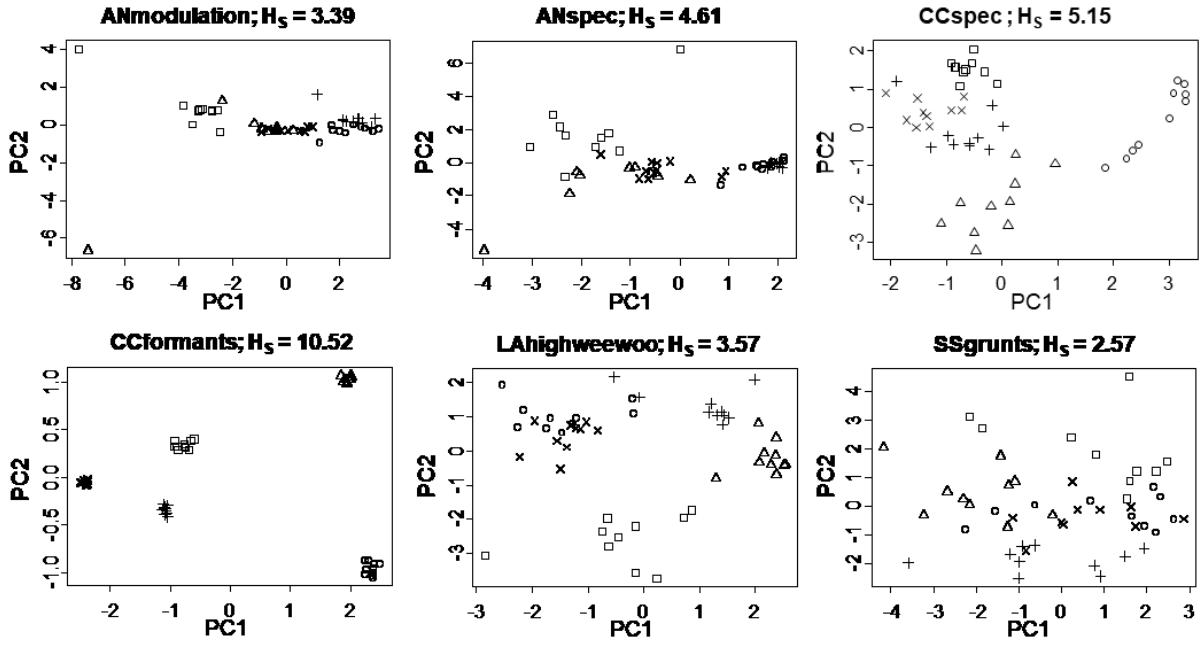


Figure 2. Illustration of empirical datasets. Five individuals were randomly sampled from each dataset of 33 individuals and all 10 calls per individual were selected. H_S for a full dataset is shown. Data were centered and scaled and subjected to PCA. The first two Principal Components are plotted.

Statistical analysis

The relationship between a given identity metric and each of the parameters was assessed graphically by plotting the mean value and the 95% confidence intervals of an identity metric against all of the modelled data parameters separately. We then used a one-way ANOVA to test whether an identity metric was constant across all levels of a parameter. One-way ANOVA along with graphical evaluation of relationships between metrics and model parameters was preferred over multivariate regression because it simply, but adequately, addresses our main question (i.e., does the metric change in response to model parameter?) without the need to specify and compare many different multivariate regression models. If we found significant differences, we followed up these with post-hoc Tukey tests to identify which parameter levels differed. Due to the large number of comparisons, we only reported comparisons of neighboring parameter levels. We used linear and non-parametric loess regression to convert H_S to DS and vice versa. Loess regression identifies a function that best describes complex data by fitting simple models to sequential subsets of data. Its main advantage is that it does not require specifications of the function and, hence, it is suitable for modeling of complex relationships. Loess regression included the number of individuals and the number of calls per individual as additional predictors. We used Spearman correlation coefficients to quantify between-metric consistency of ranking individuality in datasets. Pearson correlations were used to assess consistency within identity metrics in full and partial datasets. We then used Friedman tests, followed by a series of Wilcoxon tests (for post-hoc comparison of differences between levels), to compare correlation coefficients obtained for each pair of the metrics.

Results

The comparison of available univariate and multivariate metrics to an ideal metric is shown in Table 2.

	zero	limit	id	cov	p	o	i	points	pros	cons
Univariate Metrics										
ideal	**y**	**n**	**+**			**ns**	**ns**	**5/5**		
F	y	n	+			+	ns	4/5		sample dependent
$PIC_{betweentot}$	y	n	+			ns	ns	5/5	intuitive and straightforward calculation; allows separate assessment of within and between individual variation	not meaningful for variables with positive and negative values; cannot be summed or averaged over different variables = univariate only
$PIC_{betweenmeans}$	n	n	+			ns	ns	4/5		Converges to non-meaningful value for no individuality in data
H_{Sntot}	y	n	+			ns	-	4/5		sample dependent; incorrect HS variant
$H_{Snpergroup}$	y	n	+			ns	ns	5/5	standard variant of HS; univariate and multivariate	
$H_{Sngroups}$	y	n	+			+	-	3/5		sample dependent; incorrect HS variant
$H_{Svarcomp}$	y	n	+			ns	ns	5/5	allows including various covariates in mixed models	values twice as big as in case of standard HSnpergroup
Multivariate Metrics										
ideal	**y**	**n**	**+**	**-**	**+**	**ns**	**ns**	**7/7**		
DS	n	y	+	-	+	+	-	3/7	population and individual metric; the most commonly used metric	sample dependent; not suitable for high individuality signals because values are limited from the top
H_S	y	n	+	-	+	ns	+	6/7	univariate and multivariate; partial sample dependance is introduced by PCA but can be to large extent eliminated; biologically meaningful - provides number of unique individual signatures within population; good theoretical framework for both discrete and continuous individuality traits	partially sample dependent
H_M	y	n	+	ns	ns	ns	ns	5/7	sample independent; various types of similarity metrics can be potentially used (euclidean distances, Jaccard similarity, string edit distance, dynamic time warping, etc.)	number of independent variables needs to be known to calculate total idenity information
MI	n	y	+	-	+	-	+	3/7	could be applied with various classification methods	sample dependent; not suitable for high individuality signals because values are limited from the top

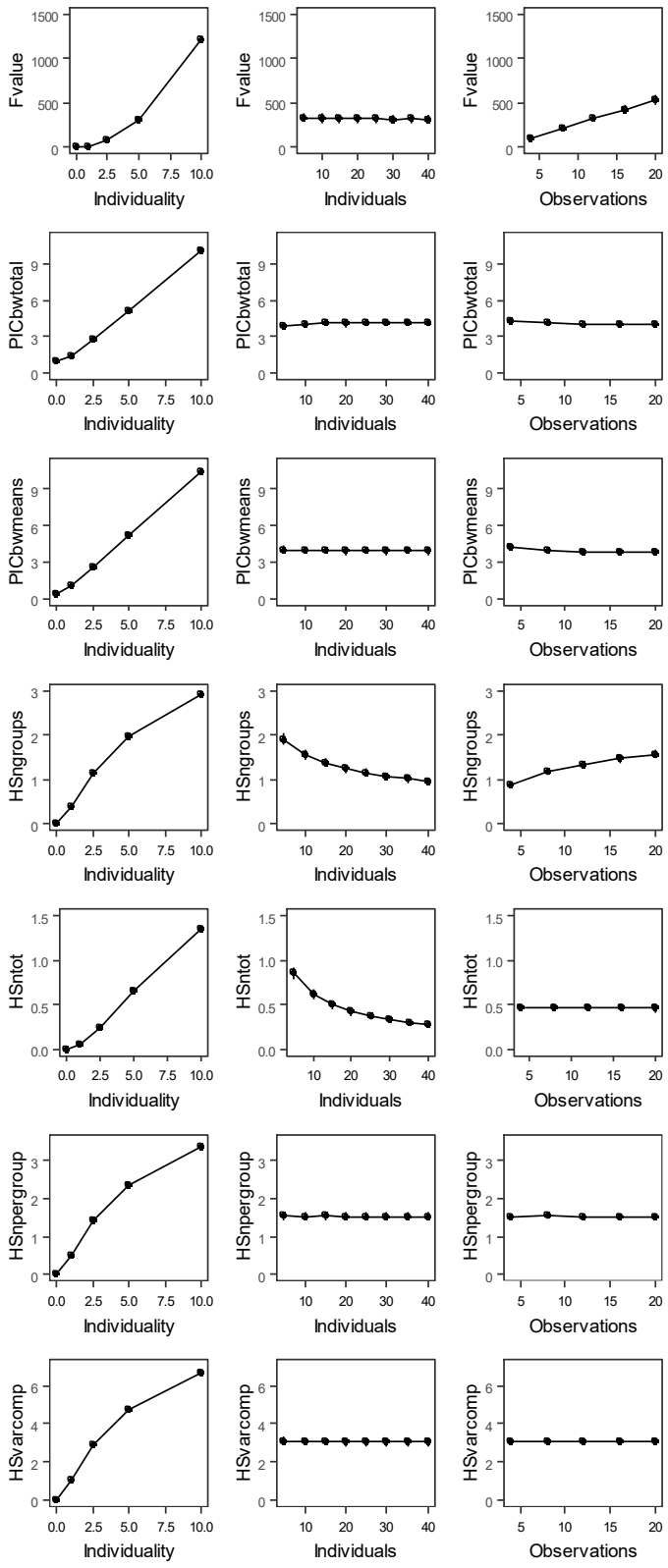
'zero' – metric has a meaningful zero; 'limit' – metric is limited from the top by an asymptote; 'id' – change in response to increasing identity information in data; 'cov' – response to increasing covariance between variables; 'p' – response to increasing number of variables; 'o' – response to increasing number of calls per individual; 'I' – response to increasing number of individuals; 'y'- yes; 'n' – no; '+' – increase; '-' – decrease; 'ns' – not significant, does not change with a parameter.

Table 2. The comparison of available univariate and multivariate metrics to a hypothetical ideal metric and summary of their pros and cons. We summed the number of matches (points) to compare different metrics to the ideal metric.

Univariate metrics

All explored univariate metrics increased with increasing individuality in the data. However, only $PIC_{betweentot}$, $PIC_{betweenmeans}$, $H_{Snpergroup}$ and $H_{Svarcomp}$ estimates were independent of the number of calls and the number of individuals used to calculate the metric (Figure 3). These general patterns were qualitatively identical when all simulated data were pooled or if only one of the parameters (number of calls, number of individuals, individuality) was changed at a time and the others were kept constant at the middle value (see Supplement 3 for detailed results including ANOVA tests).

All four sampling-independent metrics ($PIC_{betweentot}$, $PIC_{betweenmeans}$, $H_{Snpergroup}$ and $H_{Svarcomp}$) were highly correlated (Spearman correlation, all r > 0.99). $H_{Snpergroup}$ and $H_{Svarcomp}$ correctly converged to 0 in the case when individuality was set to be negligible (id = 0.01), while $PIC_{betweentot}$ and $PIC_{betweenmeans}$ converged to higher values (1.01 and 0.32 respectively). $PIC_{betweentot}$ reflects the number of potential individual signatures within a population in same way as 2^{H_S} does (Beecher, 1989), and, both, $PIC_{betweentot}$ and $2^{H_{Snpergroup}}$ reflect the ratio of between to within individual variation. Hence, convergence of $PIC_{betweentot}$ to 1 could be also seen as desirable quality and meaningful value for a signal with no individuality. $H_{Svarcomp}$ was equal to 2 * $H_{Snpergroup}$ (see Supplement 4 for details). We further considered only the $H_{Snpergroup}$ variant in multivariate analyses.



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248 **Figure 3.** Variation in univariate identity metrics in response to simulated dataset parameters:

249 individuality, number of calls per individual, and number of individuals. Means and 95% confidence

intervals are shown. Graphs were plotted using all simulated univariate data pooled together. For the graphs with only a single parameter changing at a time see Supplement 3.

Multivariate metrics

The performance of multivariate identity metrics is illustrated in Figure 4. All metrics increased with increasing individuality. DS, H_S, and MI increased with increasing number of variables available and decreased with increasing covariance between variables. Only H_M did not change in response to increasing the number of individuals. H_S and H_M did not change in response to increasing the number of calls per individual. These general patterns were qualitatively identical when all simulated data were pooled or if only one dataset parameter was changed at a time and others were kept constant at the middle value (see Supplement 5 for detailed results including ANOVA tests).

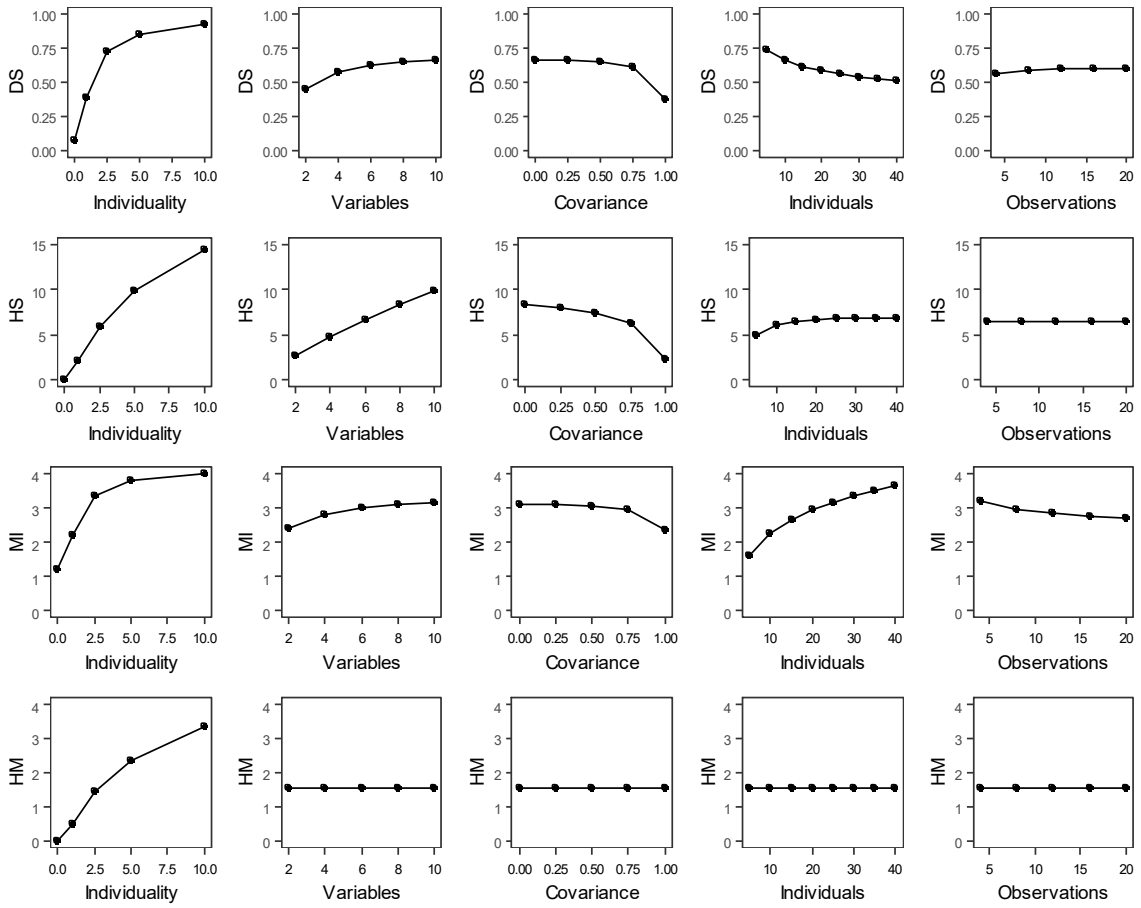


Figure 4. Multivariate identity metrics in response to simulated dataset parameters: individuality, covariance between variables, number of variables, number of calls per individual, and number of individuals. Means and 95% confidence intervals are shown. Graphs were plotted using all simulated multivariate data pooled together. For the graphs with only a single parameter changing at a time see Supplement 4.

Despite the different response of metrics to some of the simulated parameters, there was still moderate to high agreement among metrics about identity content in the data (Spearman correlations, mean r ± SD = 0.82 ± 0.07; minimum r = 0.71 for correlation between DS and MI; maximum r = 0.95 for correlation between DS and H_S). H_S had the greatest correlations with other metrics (average R = 0.88). We found no advantage to using H_M over H_S as previously suggested. Instead, H_M was equal to H_S per variable ($H_M = H_S / p$) in data with zero covariance between variables. (Supplement 6).

Thus, our simulations show that H_S matched the characteristics of the ideal metric in 6/7 cases, followed by H_M (5/7), DS (4/7), and MI (both 3/7) (Table 1).

Potential for removing bias in H_S

We observed no significant association between H_S and the number of individuals in the univariate case so we investigated the origin of the sampling bias in the multivariate case. This bias was only present when data were subjected to Principle Component Analysis (PCA). However, PCA is required to create uncorrelated components for H_S calculation.

It is possible that the more variables measured, the more individuals need to be sampled in order to reduce this bias. We therefore fixed the number of variables to 5, 10, and 20 (p = 5, 10, 20) and varied the ratio of the number of individuals to the number of variables 'i to p ratio' from 0.5 to 5 ('i to p ratio' = 0.5, 1, 1.5, 2, 3, 5) by using different numbers of individuals in our simulations (i = 3, 5, 8, 10, 15, 20, 25, 30, 40, 50, 60, 100 depending on number of variables and "i to p ratio"). The number of calls per individual was set to 10. Individuality and covariance were both chosen randomly in each

iteration from predefined intervals used in the earlier simulations (covariance range = [0, 0.25, 0.5, 0.75, 1]; individuality range = [0.01, 1, 2.5, 5, 10]). We used 100 iterations for each 'i to p ratio'. H_S did not rise significantly after the number of individuals reached at least the number of parameters (One-way ANOVA $F_{5, 1794} = 7.68$, $P < 0.001$; no significant differences between levels if 'i to p' ≥ 1, all p > 0.132) (Figure 5).

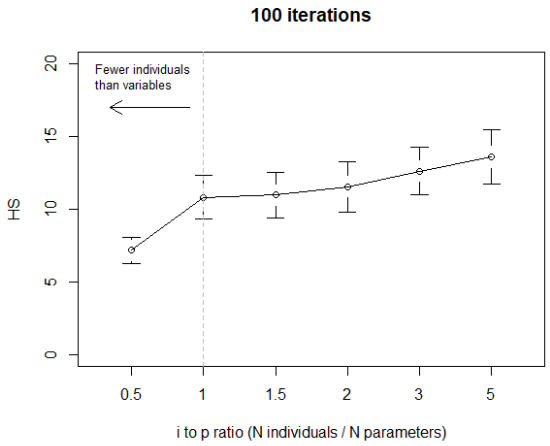
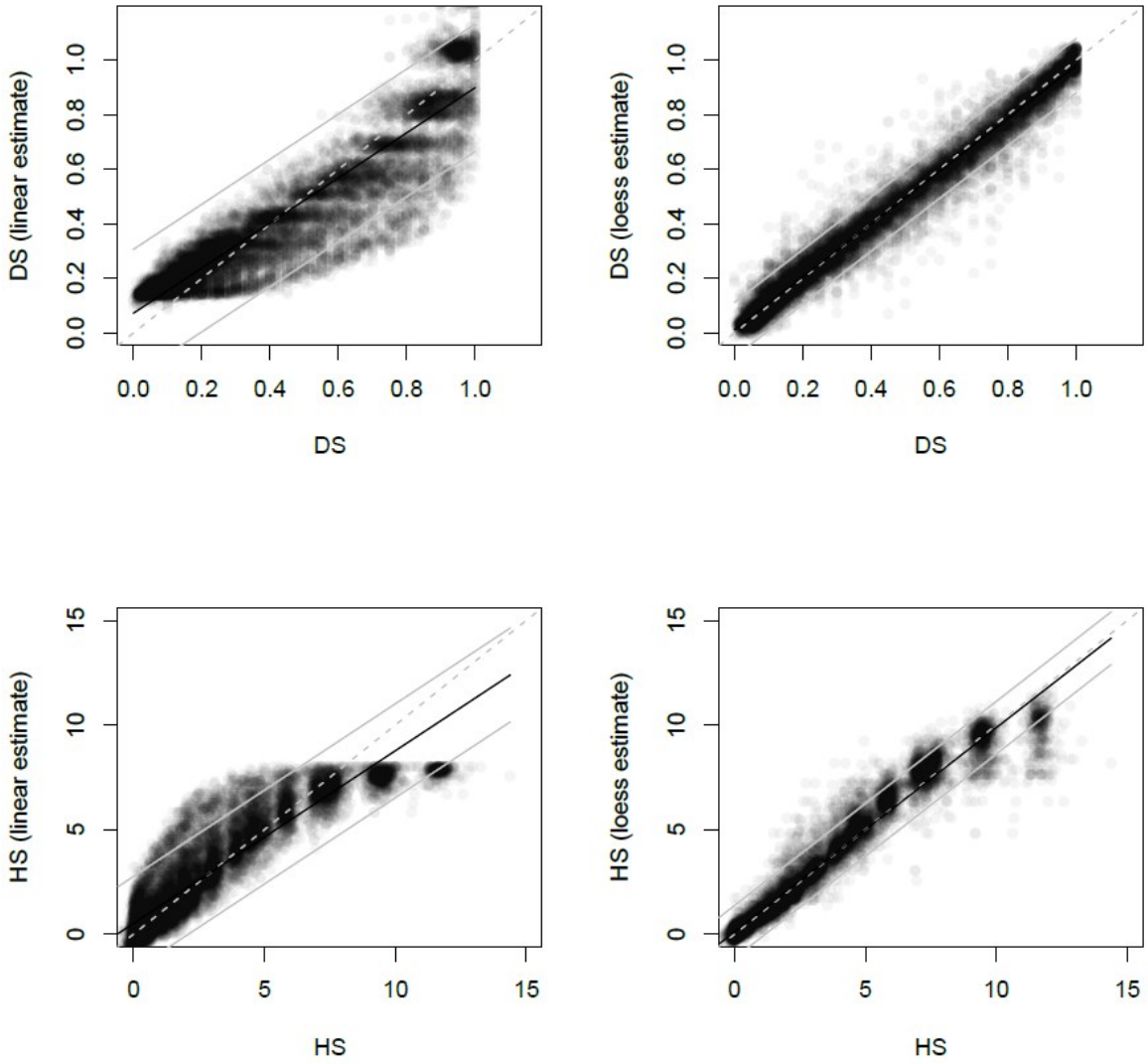


Figure 5. H_S and 'i to p ratio' (number of individuals / number of variables). H_S was under-estimated if there are fewer individuals than variables. Means and 95% confidence intervals are shown.

Converting DS to H_S and vice versa

We used simple linear regression and non-parametric loess regression to estimate H_S based on DS and vice versa. There was a previously suggested linear relationship that had a limit of $H_S = 8$ where the DS values were 100% correct discrimination (Beecher 1989). Because the H_S values in our original simulated datasets far exceeded 8, we generated a new set of simulated datasets with individuality ranging between 0.1 and 2 (id = 0.1, 0.25, 0.5, 0.75, 1, 1.33, 1.66, 2), covariance set to zero (cov = 0), number of iterations was reduced to 10 (it = 10), and other parameters were set as in previous models (p = 2, 4, 6, 8, 10; i = 5, 10, 15, 20, 25, 30, 35, 40; o = 4, 8, 12, 16, 20). These settings led to H_S values up to about 13 for data used for model building, and H_S values up to about 14 in the case of data used for model testing. These values are much closer to 8 and also much closer to H_S values reported from nature.

306 Loess models took into account the number of calls per individual and the number of individuals.
307 We compared the loess conversion and linear conversion models of DS and H_S. In general, loess
308 estimates were closer to the ideal prediction (intercept = 0, beta = 1) and the loess model reduced
309 error of both DS and H_S estimates to about a half compared to linear estimates (Figure 6). Both H_S
310 estimates were underestimated for high values of H_S. The ceiling value is clearly apparent for linear
311 estimates of H_S. It is still visible in case of loess estimates but loess predictions remain reasonably
312 good up to about H_S = 10.



313
314 **Figure 6.** Estimation of H_S and DS based on linear and loess transformation of DS and H_S respectively
315 for datasets with H_S up to 14.4. **Linear DS estimation**: Intercept = 0.07, Beta = 0.83, R^2 = 0.83,

316 Standard Error of Estimate (SEE) = 0.12, 95% Prediction interval = predicted value ± 0.23; **DS loess**
317 **estimation:** Intercept = 0.01, Beta = 0.98, R^2 = 0.97, Standard Error of Estimate (SEE) = 0.05, 95%
318 Prediction interval = predicted value ± 0.10. **Linear H_S estimation**: Intercept = 0.51, Beta = 0.83, R^2 =
319 0.83, Standard Error of Estimate (SEE) = 1.14, 95% Prediction interval = predicted value ± 2.24; **HS**
320 **loess estimation:** Intercept = 0.11, Beta = 0.98, R^2 = 0.95, Standard Error of Estimate (SEE) = 0.64,
321 95% Prediction interval = predicted value ± 1.26.

322 ## Correlations between calculated and estimated metrics

323 We were further interested in how H_{Sest} and DS_{est} might represent H_S and DS of a particular sample of
324 individuals or H_{Sfull} and DS_{full} of the whole population. For this purpose, we first generated 50 full
325 datasets with different identity levels representing 50 hypothetical populations of different species.
326 Each dataset comprised 40 individuals, 20 calls per individual, and 10 parameters. For these datasets,
327 individuality was set randomly ranging between 0.2 – 2 (0.1 increments), and the covariance was set
328 randomly ranging between 0.2 – 0.8 (0.1 increments). These settings generated datasets with H_{Sfull}
329 values that ranged from 0.22 – 9.89 (mean ± sd: 4.72 ± 2.95). Then, we repeatedly subsampled full
330 datasets to get partial datasets which simulated different sampling of the population. We
331 subsampled 5-40 individuals and 4-20 calls per individual per dataset in each of total 20 iterations.
332 We also repeatedly subsampled our empirical datasets. We subsampled 5-33 individuals and 4-10
333 calls per individual per dataset in each of total 20 iterations. The number of parameters was not
334 randomized – we always kept the original number of variables.

335 In simulated datasets, H_S and H_{Sest} were correlated almost perfectly with each other and with
336 H_{Sfull} (all average Pearson r > 0.97). There was no difference among the correlation coefficients from
337 correlations between H_{Sfull}, H_S, and H_{Sest} (Friedman Chi Square = 3.6, p = 0.165). In empirical datasets,
338 H_S calculated on partial datasets still reflected the H_{Sfull} almost perfectly (average Pearson r = 0.99).
339 While H_{Sest} reflected H_S of partial dataset (average Pearson r = 0.90), and H_{Sfull} (average Pearson r =
340 0.88) slightly worse, it remained a reasonable fit. However, H_{Sest} did not reflect H_{Sfull} as precisely as it
341 did H_S (Friedman Chi Square = 33.6, p < 0.001, post-hoc test: H_S - H_{Sfull} vs. H_{Sest} - H_{Sfull}, p < 0.001).

DS in simulated datasets was almost perfectly correlated with DS_{est} (average Pearson r = 0.99). Although the relationship between DS in full datasets (DS_{full}) and DS and DS_{est} was significantly worse (Friedman Chi Square = 40.0, $p < 0.001$; both post-hoc tests: $p < 0.005$), these associations remained strong (DS_{full} and DS: average Pearson r = 0.95; DS_{full} and DS_{est}: average Pearson r = 0.96). In empirical datasets, the correlation between DS and DS_{est} was lower than in case of artificial datasets (average Pearson r = 0.91). DS and DS_{est} of partial datasets had comparable correlations to DS_{full} (DS_{full} and DS: average Pearson r = 0.88; DS_{full} and DS_{est}: average Pearson r = 0.86). Thus, the performance of DS and DS_{est} to reflect each other or DS_{full} did not differ (Friedman Chi Squre = 0.9, p = 0.638).

Discussion

We provided an overview of the metrics used to quantify individual identity in animal signals in order to identify the best method for reporting individuality in animal signals. Biases associated with some of the commonly used metrics, and the use of different metrics across studies, makes it difficult to compare results and integrate the accumulated knowledge from the numerous published studies on individual identity in animal signals. We show that the assessment of individual identity is relatively straightforward when considering a single trait (univariate case). Both, PIC ($PIC_{betweentot}$) and H_S ($H_{Snpergroup}$), performed according to expectations. Multivariate identity metrics based on direct quantification of between to within individual variation ratios (H_S, H_M) performed better than the metrics derived from discrimination of individuals (DS, MI). We confirmed sampling-associated biases where they were reported previously (DS), but we found them even in metrics that had been developed to overcome these biases (H_S, MI). We also described yet unrecognized issues (the need to assess dimensionality for H_M to quantify the total individuality of a signal). We further found that some metrics created values that were so close that they could be viewed as redundant (PIC and H_S; H_M and H_S) and using them simultaneously brings unnecessary confusion to the field.

Based on our review and systematic analysis, we suggest H_S should be routinely reported as the standard individual identity metric because it performed closest to an ideal identity metric in the univariate, as well as in the multivariate case. The partial bias in H_S caused by the number of

individuals in a study could be removed by having at least the same number of individuals as the number of variables. H_S was the most consistent metric and correlated the best with DS and other identity metrics. Further, H_S could be converted reliably into DS if needed.

The robustness of H_M towards sampling bias (number of individuals, number of calls, as well as the number of variables and covariance) is an attractive feature. However, as we show, H_M quantifies identity information per variable and not the identity information of the entire signal. It is necessary to know the effective number of variables to calculate the total identity information of a signal (i.e., if there is perfect covariance between the variables, the effective number of variables is 1 no matter how many variables are used), which may be difficult to assess. On the other hand, H_M uses distances (similarity scores) of samples to calculate individuality and, hence, it could be potentially used not just with Euclidean distances (Searby & Jouventin, 2004, this study) but also together with other various methods assessing similarity (e.g., cross-correlation, dynamic time warping, or string edit distances).

Mutual information (MI) is derived from a confusion matrix of discrimination analysis and we show it has similar shortcomings as discrimination scores. Our results that found systematic biases in MI are in line with previous studies that investigated measures of clustering for various machine learning purposes where potentially unbiased variants of MI are constantly searched for (e.g., Amelio & Pizzuti, 2017).

Identity metrics in comparative analyses. We show that biases associated with DS (the most often used metric) and H_S (the best metric) are not necessarily fatal for comparisons of different published studies because H_S and DS values that are based on an entire population or subsamples from a population were well correlated in both simulated and empirical datasets. Additionally, the conversion of sample biased DS values into less biased H_S values could allow better comparisons between studies. Both H_S and H_M values were previously found to correlate well with DS (Beecher, 1989; Searby & Jouventin, 2004). We extend previous findings for H_S (Beecher, 1989) to situations

393 with unequal sampling and we show it is possible to convert between H_S and DS with an acceptable
394 amount of error even when datasets differ in the number of individuals and calls per individual, and
395 have important issues associated with multivariate normality (Supplement 2). Discriminant analysis
396 (DA) and Principal component analysis (PCA) used for DS and H_S calculations both assume
397 multivariate normality for optimal results. While using these methods with non-normal data cannot
398 be, in general, recommended, relatively high correlations between our metrics in empirical datasets
399 suggest that DA and PCA scores were quite robust to these normality issues. Discrimination and
400 dimensionality reduction analytical techniques that are able to handle normal and non-normal data
401 definitely need to be considered in future individual identity studies.

402 **Future individual identity metrics.** We hope that our study will stimulate further discussions
403 about how individual identity should be properly measured. Although we suggest that H_S should be
404 generally used to quantify individuality, different metrics or more complex approaches might be
405 required for particular interesting questions. For example, H_S can only provide a population estimate
406 of individual identity. Researchers might be interested in whether distinctiveness of individuals
407 increases during ontogeny (Syrová et al., 2017). In this case, discrimination scores can be reported for
408 each individual, thus making statistical evaluation possible. Furthermore, separate assessments of
409 within- and between individual variations when calculating PIC might be useful to test hypotheses
410 about which of the two has been selected for. Within-individual variation could be reduced by, for
411 example, ritualized behavior while between-individual variation could be increased through, for
412 example, morphological variation in structures producing or carrying the signal (e.g., Sheehan &
413 Nachman, 2014). The dimensionality of identity signals might be an important factor for recognition
414 processes (Trunk, 1979) and evolution could favor low dimensional signals. Paralleling the
415 distribution of individuals in space (territoriality, living in colonies), individual signatures within a
416 population, too, could have random, clumped, or regular distributions depending on the mechanisms
417 behind individual distinctiveness and the degree of plasticity of identity signals.

We evaluated the efficacy of all metrics within the acoustic modality only. It is increasingly recognized that signals may employ multiple modalities (Partan & Marler, 1999; Partan, 2013). All of the identity metrics discussed here could be, in principal, used in visual or chemical domains as well. H_S has an advantage that it could be used both for discrete traits, such as color variants, presence of particular alleles or chemicals, and for continuous traits such as size of visual patterns, duration of calls, etc. (Beecher, 1982, 1989). However, identity information outside the acoustic domain has been rarely quantified and meaningful comparison of individual identity across modalities remains a challenge for the future.

It is likely that automatic data collection and analysis techniques will be increasingly applied for various recognition tasks, including individual recognition (Elie & Theunissen, 2018; Stowell, Petrusková, Šálek, & Linhart, 2019). While these methods will allow studying individual identity signalling on unprecedented scales and sample sizes, the resulting classification accuracy scores will be analogous to the discrimination score, with similar positives and drawbacks.. However, many different feature sets, pre-defined or automatically derived from data, as well as many different classification methods could be combined to test for the robustness of identity signals and/or to mimic and test for different alternatives of possible real recognition processes (Elie & Theunissen, 2018).

Conclusion. We suggest that, at the current state of knowledge and methodology development, H_S should be generally reported as the the “golden standard” individual identity metric to allow the best comparison of individuality in signals across different studies. Given that H_S may not be sufficient in all cases, we encourage further research to develop new metrics to quantify identity information in signals. However, new metrics should always be appropriately assessed and their performance directly compared to the best existing metrics. We provide datasets and scripts that should help to assess individual identity information in animal signals and benchmark the future metrics.

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Authors' contributions

PL and DTB conceived the ideas and designed methodology; PL, TO, MB, MŠá, MŠp, MS, and RP collected the data; PL analysed the data; PL and DTB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility statement

Data and code used for this article are available within IDmeasurer R package currently available on CRAN (https://cran.r-project.org/web/packages/IDmeasurer/index.html) and GitHub (https://github.com/pygmy83/IDmeasurer).

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