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Pyow but not hack calls of the male putty-nosed monkey (*Cercopithcus nictitans*) convey information about caller identity

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Summary

Individual differences within the acoustic structure of vocalisations have the potential to inform signal receivers about the identity of the caller. Such differences can often be explained by morphological differences of the signaller's sound production apparatus. Natural selection may have favoured individual variation within call types, especially if identity cues enhance call function. In addition, animals may modify their vocalisations such that they sound more similar to, or more distinct from those of neighbouring conspecifics. We recorded pyow and hack vocalisations from five recognised male putty-nosed monkeys (*Cercopithecus nictitans*) in Gashaka Gumti National Park, Nigeria. We analysed the temporal and spectral features of both call types to investigate whether the calls contained identity cues, and whether calls of neighbouring males were less or more different in their acoustic structure than expected by chance. More parameters were found to vary significantly between individuals within pyows than hacks, and whilst pyows could be correctly assigned to individual callers more often than would have been expected by chance, hacks could not. We found no relation between geographic distance and acoustic similarity of pyows and hacks.

Keywords: *Cercopithecus*, vocalisations, individual differences, caller identity, acoustic analysis.

Introduction

Variation between individuals in the acoustic structure of a single call type can convey important social information to signal receivers (Bradbury &

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Vehrencamp, 1998). Studies across a wide range of species have investigated individual differences in signal structure within different call types and suggested that this variation has the potential to inform receivers about the signaller's sex (Norcross & Newman, 1993; Blumstein & Munos, 2005), age class (Wanker & Fischer, 2001; Fischer et al., 2002), rank or fitness (Reby & McComb, 2003; Kitchen et al., 2003), kin group (Masters et al., 1995; Rendall et al., 1996), population or social group (Mitani et al., 1992; Castellano et al., 2002) and individual identity (Marler & Hobbett, 1975; Macedonia, 1986; Butynski et al., 1992; Jones et al., 1993; Hammerschmidt & Todt, 1995; Owren et al., 1997; Steenbeek & Assink, 1998; Teixidor & Byrne, 1999; Semple, 2001; Frommolt et al., 2003).

Some individual differences may result from restrictions imposed on signal structure by the signal production mechanism (Hauser, 1996). The source/filter theory of sound production describes how the larynx (source) and the supralaryngeal vocal tract (filter) function to produce sound, and appears to be relevant to all mammalian species studied so far (Fitch, 2000). Individual differences in the size and shape of the caller's larynx and supralaryngeal vocal tract may result in differences in the acoustic structure of their calls, especially in the position of fundamental and formant frequencies (Fitch, 1997; Rendall et al., 2005).

Call function has also been implicated in the evolution of identity cues. For signallers to maximise the benefits of communication, it may be necessary to ensure that receivers distinguish the individual identity of the caller. Consequently, it has been suggested that selection for individually distinctive vocal cues will be stronger within calls whose function depends on the identity of the caller being perceived (Bradbury & Vehrencamp, 1998). The communication of information related to caller identity is integral to the maintenance of intra-group cohesion and inter-group spacing, and many studies looking for individual differences in call structure have, therefore, focused on contact calls (Symmes et al., 1979; Maurello et al., 2000; Rogers & Cato, 2002).

There is potentially less selection pressure for the inclusion of individually distinctive acoustic cues within alarm calls (Blumstein et al., 2004, Blumstein & Munos, 2005), although selection on receivers to discriminate between individuals would allow them to respond in accordance with the reliability of the caller (Cheney & Seyfarth, 1988), and in territorial species, the proximity of threat (Hare, 1998). Whilst individually distinctive alarm

calls have been reported for some species (particularly small rodents, Leger et al., 1984; McCowan & Hooper, 2002; Randall et al., 2005) individual differences in the alarm calls of non-human primate species have often been inferred from receiver responses rather than acoustic analyses of calls (Cheney & Seyfarth, 1988; Sproul et al., 2006) and very few studies have provided evidence of such differences based on acoustic analyses (Fischer et al., 1995, 2001). Such analyses of call structure can be highly informative, as they shed light not only on whether calls are individually distinct, but also on which parameters are most relevant, or contain the necessary variability, to convey inter-individual differences.

In addition to individual differences, the geographical proximity of individuals could have an impact on the acoustic structure of their calls. Within a few avian and mammalian species, individuals are capable of modifying the form of their own calls as a result of experiencing the calls of others; this process known as production learning may lead to the convergence or divergence of neighbouring individuals' vocalisations (Janik & Slater, 1997). Whilst the occurrence of vocal production learning in primates is controversial (Egnor, 2004), regional variation in vocal communication between different populations and social groups has been identified in a few primate species (Maeda & Masataka, 1987; Elowson & Snowdon, 1994; Fischer et al., 1998; Marshall et al., 1999; Lemasson & Hausberger, 2004; Crockford et al., 2004).

Putty-nosed monkeys (*Cercopithecus nictitans*) live in groups, which typically contain one adult male, several females, and their offspring. The vocal repertoire of adult males contains three acoustically distinct loud calls, booms, pyows and hacks (Gautier & Gautier-Hion, 1977); booms are rare but pyow and hack calls are commonly produced. It has been proposed that pyows and hacks are given as part of a circadian rhythm and function to maintain intra-group cohesion and inter-group spacing (Gautier & Gautier-Hion, 1977), that they are produced in response to disturbances and function as general alarm calls (Struhsaker, 1970) and even as functionally referential alarm calls (Eckardt & Zuberbühler, 2004). Recent studies have suggested that pyows have multiple functions, including as general alarm and contact calls, whilst hacks function primarily as alarm calls (Arnold & Zuberbühler, 2006a; Arnold et al., 2008). A specific combination of the two call types labelled a pyow–hack sequence appears to function in initiating group movement (Arnold & Zuberbühler, 2006b; Arnold & Zuberbühler, 2008). Thus,

selection for the capacity to produce individually distinctive calls is likely since the identity of the caller should influence listerners' responses to those calls. These selection pressures should act predominantly on neighbouring males, whose calls are the most likely to be confused. It would be predicted, therefore, that there would be an inverse relationship between males' geographic proximity and the acoustic similarity of their calls.

Recent experiments suggest that female putty-nosed monkeys respond differently to their group male's and other males' pyow–hack sequences (Arnold & Zuberbühler, 2008). However, no studies have been carried out to investigate whether variation in individual pyow and/or hack calls of the male relate to the identity of the caller. This study aims firstly to investigate whether information about individual identity is encoded within pyow and hack calls recorded from recognised male putty-nosed monkeys, and secondly to test whether the acoustic similarity of males' calls is related to their geographical proximity.

Methods

Study site and species

Recordings were made of wild male putty-nosed monkeys within approx. 10 km^2 of the Kwano trail system, Gashaka Gumti National Park, Northeast Nigeria. This area consists primarily of semi-deciduous lowland rainforest interspersed with patches of savannah woodland (Sommer et al., 2004). At this site, putty-nosed monkeys live in groups of 13–22 individuals consisting of a single adult male, 6–9 adult females, and their offspring (Arnold & Zuberbühler, 2006a). Home-range size is estimated at <1 km^2 (Arnold & Zuberbühler, 2006a), and 3–4 groups are commonly found within 1 km^2 (Dunn, 1993).

The male's vocal repertoire contains three loud call types, but only two of these calls are commonly produced; these acoustically distinct call types have been labelled pyows and hacks. Both call types are tonal; pyows are a higher frequency call, and demonstrate a descending frequency sweep compared to the lower frequency and abrupt onset of hacks (Arnold & Zuberbühler, 2006a, Figure 1). Pyow and hack calls produced by the sole adult male of five recognised groups were recorded. For the purpose of this study, individuals were labelled 1–5.

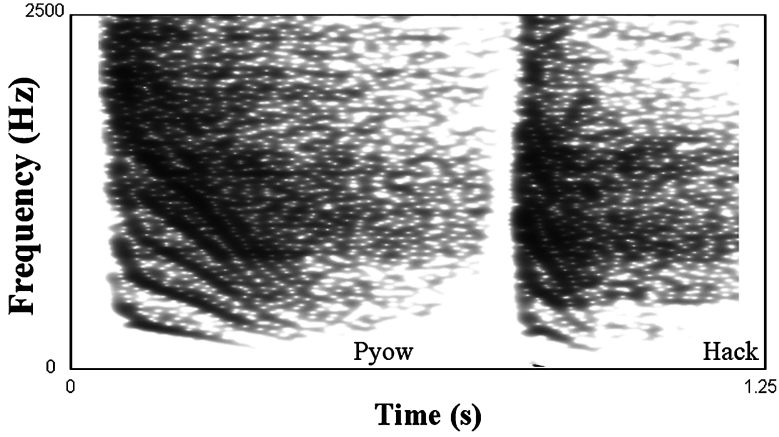

Figure 1. Spectrographic representation of a male putty-nosed monkey's pyow and hack call.

Individual identity analysis

Recording of vocalisations

Recordings were made ad libitum between 0600–1930 h from February–June 2007. It was often difficult to identify the cause of call production; whilst some calls seemed to be given in response to another individual's calls or to a disturbance, other calls appeared to be produced spontaneously. The calling bouts that were recorded for each male never occurred within an hour of each other, a maximum of three calling bouts were recorded per male on any given day, and the calls of each male were recorded over a period of 32 or more days (range of time between recordings; male 1, 73.6 $\pm$ 136.5 h; male 2, 28.9 $\pm$ 41.7 h; male 3, 68.3 $\pm$ 125 h; male 4, 70.0 $\pm$ 213.7 h; male 5, 51.2 $\pm$ 77.2 h) to ensure that call samples were independent of each other. Vocalisations were recorded using a Sennheiser MKH416 directional microphone and a Marantz PMD 671 recorder (sampling rate of 44.1 kHz, digitised at 16 bits).

Acoustic analysis

Recordings were excluded from further analysis if sound quality was too poor to extract reliable or accurate measures of acoustic parameters due to high levels of background noise ($N = 5$), equipment failure ($N = 3$) or if the male called at too great a distance from the microphone resulting in inadequate recording quality and confidence of correct identification of the target

male ($N = 12$). Calling bouts were made up of pyows only, hacks only, or a combination of both call types. The first pyow and/or hack of adequate quality within each calling bout (number of bouts; male 1, $N = 12$, male 2, $N = 13$, male 3, $N = 16$, male 4, $N = 12$, male 5, $N = 16$), was selected for analysis to minimise acoustic variation related to call position within the bout (Arnold & Zuberbühler, 2006a). This gave 10 samples of each call type per individual and an overall sample size of 50 pyows and 50 hacks. Praat version 4.5 (Boersma et al., 2006) was used to produce spectrograms of each call and to extract data on a range of parameters with the potential to encode information related to caller identity (Table 1, Figure 2). Whilst we refer to the pronounced frequency bands extracted by Praat formant tracker as formants, it should be noted that this study does not test whether these bands result from resonances in the vocal tract, or whether they are independent from F_0 and harmonic structures (Harris et al., 2006). In addition, pyows in comparison to human speech have a relatively high F_0 (around 300 Hz), so that larger sections of these calls do not contain any laryngeally-generated energy. This may have affected the accuracy of Praat's formant tracker in extracting formant frequencies.

Twenty-three measures were extracted from the spectrograms of pyows and hacks with a viewing range of 0–2500 Hz (Table 1). A narrow-band window size of 0.05 s was used for extracting measures of F_0 and a broadband window length set at 0.005 s was used for extracting measures of formant frequencies.

Statistical analysis

Statistical analyses of the ten pyows and ten hacks for each of the five males were carried out in SPSS 15.0 (SPSS, Chicago, IL, USA). For normally distributed data, one-way ANOVAs with a significance level set at 0.05 were used to investigate the degree to which variation in extracted parameters could be explained by the identity of the caller. For the single parameter that was not normally distributed (LtasDfHz) a Kruskal–Wallis ANOVA was used instead. For significant results, parametric Tukey or non-parametric Mann–Whitney post-hoc tests were used to identify which individuals differed significantly from one another. For Mann–Whitney tests the p-values of the 10 simultaneous tests (each individual compared against every other individual) were modified using a sequential Bonferroni correction to reduce

Table 1. Acoustic measurements extracted from pyow and hack calls, abbreviations used for each parameter, and a description of how each parameter was extracted from calls or calculated from other parameters.

Acoustic parameter measured	Acoustic parameter abreviation Hk/Py	Description of how acoustic parameter was measured or calculated
Duration of F_0	FoDuration	Measured by eye using cursor function
Beginning frequency of F_0	FoHzBeg	
Middle frequency of F_0	FoHzmid	
End frequency of F_0	FoHzend	
Mean frequency of F_0	FoHzmean	Mean value of beginning, middle and end Fo frequency
Rate of change in F_0 within call	FoAllrate	Calculated from beginning, middle and end Fo measures and duration of call
Rate of change in F_0 in first half of call	FoBegrate	
Rate of change in F_0 in second half of call	FoEndrate	
Intensity of F_0 at beginning of call	FoBegInts	Cursor function used to indicate absolute intensity within spectral splice of spectrogram at beginning, middle and end of call
Intensity of F_0 at middle of call	FoMidInts	
Intensity of F_0 at end of call	FoEndInts	
Mean intensity of F_0	FoMeanInts	Mean value of beginning, middle and end Fo intensities
Dominant frequency	LtasDfHz	Ltas function used to query 'Get frequency at maximum'
Mean intensity of DF	DFInts	Ltas function to query 'Get value at frequency' and inputting frequency of DF
Intensity of DF minus intensity of F_0	DFminusFoInts	Calculation of DF intensity minus Fo mean intensity
Mean frequency of formant 1	F1	'To Formant Burg' function used with max. no. of formants set at 4 and max. formant set at 2300 Hz. Mean frequency value was calculated for each formant from the extracted contours
Mean frequency of formant 2	F2	
Mean frequency of formant 3	F3	
Mean frequency of formant 4	F4	
Mean dispersion between formants 1 and 2	Disp1	F2 minus F1
Mean dispersion between formants 2 and 3	Disp2	F3 minus F2
Mean dispersion between formants 3 and 4	Disp3	F4 minus F3
Mean dispersion between all formants	MeanDisp	Mean value of Disp1, Disp2 and Disp3

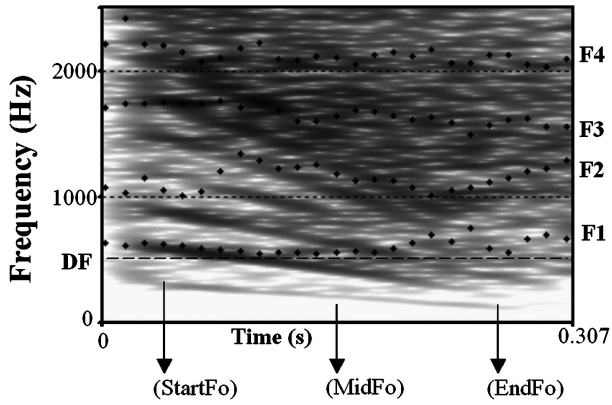

Figure 2. Spectrogram of male pyow within a narrow-band window size of 0.05 s and viewing range of 0–2500 Hz. Acoustic features are annotated in reference to procedures of acoustic analysis.

the effects of type-1 error (Rice, 1988). Within each call type, Spearman's correlation was used to investigate the relationships between acoustic parameters for which significant inter-individual variation was found.

All parameters were entered into separate stepwise discriminant function analyses for pyow and hack calls. If this analysis identified significant variation between the calls of the different males, the individual scores for the first two discriminant functions were plotted to create an ordination diagram within which points were labelled by caller identity to show the grouping of calls within individuals. A cross-validation using the 'leave-one-out' method (Mundry & Sommer, 2007) was then performed to calculate predicted caller identity for each call, and the percentage of calls correctly assigned to caller was then calculated for each individual. A binomial test with a probability value set at 0.2 (given that there were 5 males in the study) was used to test whether calls were correctly assigned to caller more often than would be expected by chance.

Geographical analysis

Calculation of geographical distances between males

A GPS was used to record the geographical positions (with an accuracy of $\pm$15 m) of each of the five males over the course of this study, using map datum WGS84 and the positions format 'degrees and decimal mins'. These readings were put into GPS Utility (GPSU) software (GPS Utility,

Southampton, UK), and a co-ordinate was calculated for each individual from the mean values of all latitudinal and longitudinal readings. Each male was then plotted onto a map using this mean co-ordinate and the distance between each male was measured.

Calculation of acoustic differences between males

For each male, mean values were calculated for all twenty-three of the acoustic variables extracted from both his pyows and hacks. Three separate principal components analyses (PCA) were then carried out. The first included the mean values of all 46 variables (23 from pyows and the same 23 from hacks), the second included the mean values of all 23 pyow variables, and the third included the mean values of all 23 hack variables. This produced three sets of 2-dimensional co-ordinates for each individual based on the acoustic values extracted from their calls. Pythagoras' rule was then applied to calculate the distances between individuals within this 2-dimensional space for each of the three data sets. This produced values of acoustic similarity for all pairs of individuals based on all their calls, all their pyows, and all their hacks.

Statistical analysis

Spearman's correlation was carried out to investigate the relationship between acoustic similarity and geographical distance between males.

Results

Acoustic parameters

Eight of the parameters extracted from pyows showed a significant effect of caller identity; some of these eight parameters were significantly correlated with each other (Table 2). There was a significant effect of caller identity on two of the parameters extracted from hacks (Table 2); these two parameters were not correlated with each other. Post-hoc tests identified which individuals differed significantly from one another within these 10 parameters (Figure 3).

Discriminant function analysis

No discrimination was made between hacks produced by different males. A significant difference was found between pyows produced by the different

Table 2. Effect of caller identity on extracted pyow and hack parameters (one-way ANOVA and Kruskal–Wallis test).

Variable	Pyow $F_{4,45}$ or χ^2_4	Hack $F_{4,45}$ or χ^2_4
FoDuration	1.831	0.578
FoHzBeg	6.517***	2.074
FoHzmid	1.473	2.267
FoHzend	1.442	1.488
FoHzmean	3.241*	2.217
FoAllrate	1.220	1.551
FoBegrate	2.893*	0.802
FoEndrate	0.267	3.266*
FoBegInts	0.775	0.234
FoMidInts	2.794*	1.926
FoEndInts	0.778	1.504
FoMeanInts	0.565	0.788
LtasDfHz	15.065**[a]	6.387[a]
DFInts	1.909	0.876
DFminusFoInts	7.539***	1.428
F1	1.989	2.030
F2	2.332	0.475
F3	2.697*	2.257
F4	0.723	1.606
Disp1	0.579	1.910
Disp2	4.603**	2.958*
Disp3	1.200	0.297
MeanDisp	1.077	1.021

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

[a] Data not normally distributed and tested with Kruskal–Wallis test. Of the parameters in pyows that showed significant variation across individuals, the following were correlated; FoHzBeg and FoHzmean ($r_s = 0.608$, $p < 0.001$), FoHzBeg and FoBegrate ($r_s = 0.334$, $p < 0.05$), FoHzmean and LtasDFHz ($r_s = 0.319$, $p < 0.05$), FoMidInts and LtasDFHz ($r_s = 0.375$, $p < 0.01$), LtasDFHz and Disp2 ($r_s = -0.478$, $p < 0.001$), DFminusFoInts and F3 ($r_s = 0.453$, $p < 0.01$), DFminusFoInts and Disp2 ($r_s = 0.298$, $p < 0.05$), F3 and Disp2 ($r_s = 0.632$, $p < 0.001$).

males (Wilks' Lambda = 0.27, $p < 0.001$) with PyFoHzBeg, PyDFminusFoInts and PyDisp2 having significantly different means across the groups.

A scatter-plot using discriminant function scores for the first (explaining 75.1% of the variance; eigenvalue = 1.44) and second (explaining 19.9% of the variance; eigenvalue = 0.38) axes, and overlaid with identity information to illustrate the clustering of pyows in relation to caller identity is shown in Figure 4.

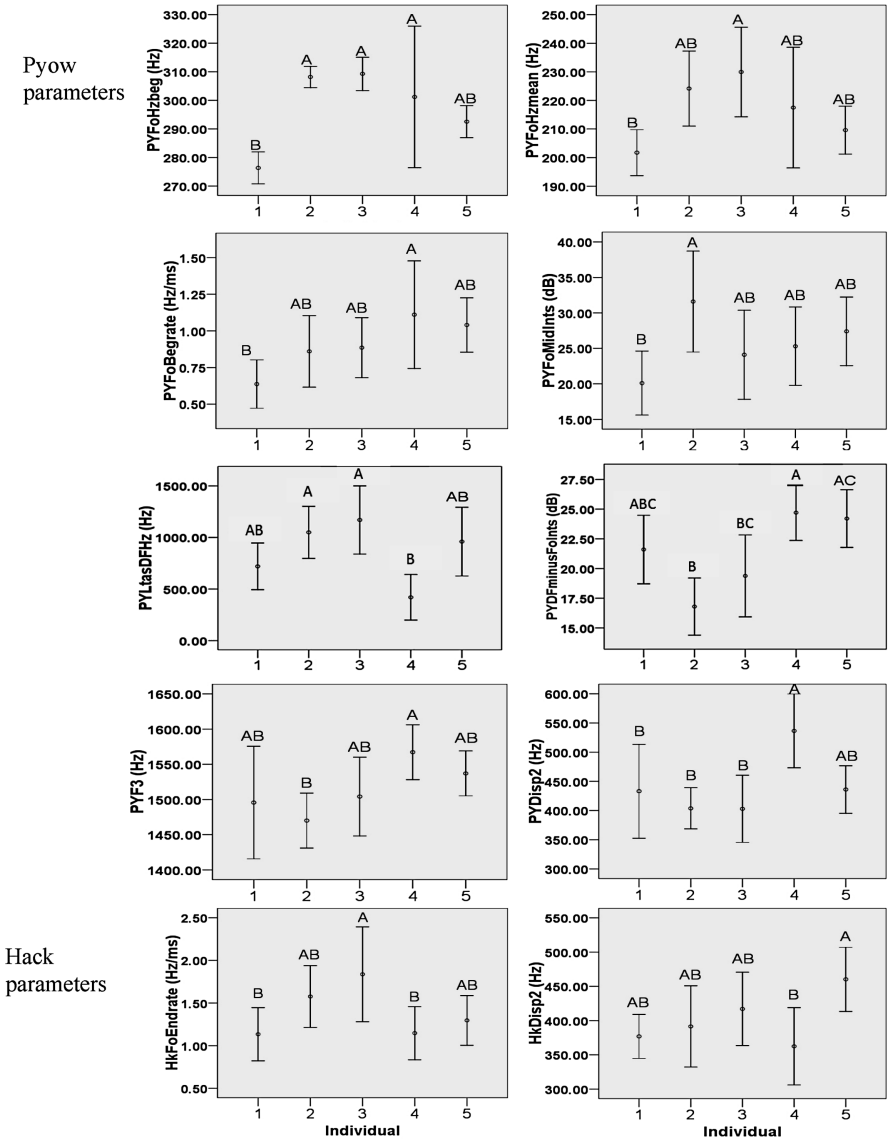

Figure 3. Variation in the ten call parameters that identified significant variation between individuals. The *y*-axis is an abbreviation of the parameter measured, the *x*-axis gives the caller's identity, and the error bars show the mean value with 95% confidence intervals. Individuals with the same letter above their error bar are not significantly different (post-hoc Tukey tests $p < 0.05$, Mann–Whitney p-values modified for 10 simultaneous tests using sequential Bonferroni correction).

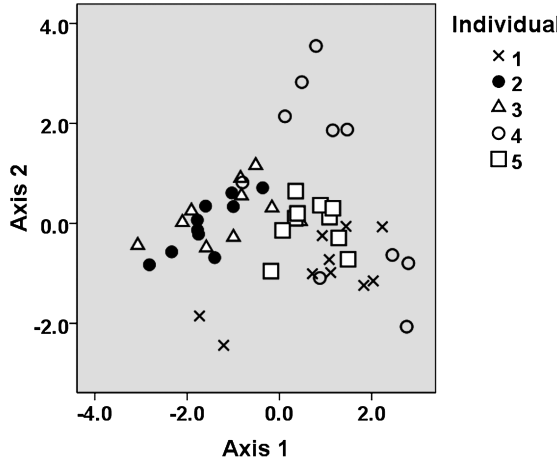

Figure 4. Scatter plot using the first two discriminant functions of the pyows of five adult male putty-nosed monkeys showing scores from 3 pyow parameters, overlaid with caller identity.

Table 3. Percentage of pyow calls assigned correctly to caller through 'leave-one-out' cross-validation.

Individual	Percentage of pyows allocated to the correct individual
1	70
2	60
3	30
4	10
5	70

A cross-validation correctly identified individual males' pyows in 10–70% of cases (Table 3). Pyows were correctly assigned to caller more often than would be expected by chance (Binomial test, pyows $N = 50$, $p < 0.001$).

Comparing acoustic similarity with geographical distance

There was no correlation between the proximity of males and the acoustic similarity of their pooled pyow and hack calls ($r_s = -0.036$, $N = 10$, $p = 0.921$), the acoustic similarity of their pyows ($r_s = 0.208$, $N = 10$, $p = 0.564$), or the acoustic similarity of their hacks ($r_s = -0.049$, $N = 10$, $p = 0.892$).

Discussion

The results of this study suggest that male putty-nosed monkeys provide sufficient information within the acoustic structure of their pyows for receivers to differentiate between the calls of different individuals, but that hacks are not individually distinctive. There was no correlation between the geographical distance between males and the acoustic similarity of their calls, suggesting that neighbouring males' calls were no more or less similar than expected by chance.

This study found that within both call types significant variation across individuals was found within measures related to the position of the F_0 and spectral energy peaks (formant related measures within both call types, and within pyows, measures relating to the dominant frequency), indicating individual differences in the production and filtering of sound.

Within acoustic parameters found to vary significantly between individuals, one or at most two individuals differed significantly from the other individuals, making it unlikely that the identification of individuals' calls would depend on perception of differences within a single parameter. A discriminant function analysis, identifying patterns of call clustering based on a suite of parameters, suggested that information relating to caller identity might be encoded within more than one acoustic parameter. Playback experiments using modified call exemplars would be required to test which parameters if any are relevant to receivers' perception of individual differences (Ceugniet & Izumi, 2004; Miller & Hauser, 2004).

Stepwise discriminant function analyses found pyows but not hacks to be correctly assigned to caller significantly more often than would be expected by chance. Differences in larynx and vocal tract morphology will affect the acoustic structure of vocalizations to a greater extent within calls consisting of harmonically rich frequency spectra and broadband random noise (Owren et al., 2003). However, pyow and hack calls are similar in overall acoustic structure (Arnold & Zuberbühler, 2006a) suggesting that alternative explanations need to be sought for the difference between these call types in their degree of individuality.

One possible explanation is that pyows may be more individually distinctive than hacks as a non-adaptive byproduct of call duration. Pyows are significantly longer than hacks (Arnold & Zuberbühler, 2006a), which may translate into more opportunities for individual differences to show. Alterna-

tively there may be stronger selection pressures for individuality within pyows than within hacks. It has been suggested that pyows are a multifunctional call, aiding intra- and inter-group communication, and alerting group members to potential danger (Arnold & Zuberbühler, 2006a; Arnold et al., 2008). Identity cues within these social contexts would be beneficial, as appropriate responses of signal receivers would depend on whether the caller was in their social group, belonged to a neighboring group or was an unfamiliar male. It has been suggested that hacks function as alarm signals (Arnold & Zuberbühler, 2006a; Arnold et al., 2008). Whilst some advantages have been proposed for signal receivers to recognize the individual identity of alarm callers (Hare, 1998), information about individual identity may be relatively less important in the case of alarm calls than socially functioning calls since receivers should respond to an alarm signal irrespective of the identity of the caller (Bradbury & Vehrencamp, 1998).

The idea that call function may have an effect on the degree to which call types are individually distinct is supported by a study of rhesus macaque (*Macaca mulatta*) vocalizations. Coo calls, which function in maintaining intra-group contact, were the most individually distinctive call type. Grunts, which function in mediating face-to-face social interactions, were less individually distinctive. Screams, which are given in aggressive interactions and thought to function in recruiting aid, were least distinctive and could not reliably be assigned to caller (Rendall et al., 1998). These differences in individuality may be related to the extent to which signalers need to encode identity in order for receivers to respond appropriately (Rendall et al., 1998).

The finding that geographical proximity of males was not related to the acoustic similarity of their calls suggested that even though their territories could overlap, male putty-nosed monkeys did not modify their calls in response to the experience of hearing the calls of neighboring males. It is possible that the strong individuality present in males' pyows negates a need for further divergence between the calls of neighboring animals. In addition, natural selection may act on receivers to distinguish between existing differences, as opposed to on callers to increase the distinctiveness of identity cues. If male putty-nosed monkeys are incapable of learned modifications to their loud calls, then the former explanation seems more plausible.

Individual recognition plays an integral role within dominance hierarchies, coalitions and reciprocal alliances (Bradbury & Vehrencamp, 1998), whilst known/unknown systems allow individuals to respond preferentially

to a single known individual. A previous study on this putty-nosed monkey population indicated that females responded to the pyow-hack sequences of their own group male by moving toward the caller, but did not respond similarly to the pyow–hack sequences of extra-group males (Arnold & Zuberbühler, 2008). Playback experiments to evaluate the perception of both call types by conspecifics would be useful to investigate whether receivers perceive the inter-individual differences identified in this study, and if so to investigate whether perception resembles a system of individual recognition or a system whereby receivers differentiate between the vocal signals of known and unknown signalers.

Finally, as pyows and hacks are frequently emitted in sequences and studies suggest that important information is conveyed within at least one call combination (Arnold & Zuberbühler, 2006b; Arnold & Zuberbühler, 2008), further studies should investigate the potential for individuality within call sequences in order to assess whether these, as well as the component calls within them, reveal information about the identity of the caller.

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