METHODS

Studying shape in sexual signals: the case of primate sexual swellings

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Abstract Despite extensive research on animal signals,
their shape has been largely overlooked compared to other
components such as size or colour. This may represent a
substantial gap in our understanding of animal communi-
cation, since shape perception is believed to influence
various processes in behavioural ecology, from prey–
predator interactions to mate recognition. The technical
challenge of measuring shape may explain this bias. This
study introduces a morphometric method for the analysis of
shape in animal signals and applies it to the study of
patterns of shape variation in a classical sexual signal: the
sexual swellings of female primates. Using elliptic Fourier
descriptors (EFDs), we derived quantitative estimates of the
two-dimensional shapes of sexual swellings in two primate
populations: wild chacma baboons (*Papio ursinus*) from
Namibia and captive mandrills (*Mandrillus sphinx*) from
Gabon. Despite intra-specific variability, the two species
exhibited consistently different swelling shapes. Within
species, our analysis further showed more variation in
swelling shape between females than across consecutive
oestrous cycles of the same female. Using human judges,
we confirmed that individual shape differences were
visually detectable within both species. Finally, the relation-
ships between individual traits and swelling shape were
investigated, revealing age-associated variation in swelling
shape in both species. Our study illustrates the high

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potentialities of EFDs to analyse patterns of shape variation at various scales: not only between species but also between and within individuals.

Introduction

Animal signals, traits that are thought to be specialised for the purpose of communication, are used in a variety of contexts, from warning potential predators against low palability to finding the best mate (e.g. Johnstone 1997). They exploit a wide array of sensory modalities including visual, olfactory, acoustic and tactile cues. Yet, despite the substantial body of work focusing on signal design and evolution, the shape component of animal signals, which can be perceived through both visual and tactile senses, has been largely overlooked in comparison to other components, such as size or colour.

The potential importance of shape perception in animal behaviour is suggested from a variety of contexts. For instance, several studies suggest that predators identify their prey through shape (Kauppinen and Mappes 2003; Catania et al. 2008), thus also confirming the intuitive idea that signal shape may be essential in mimicry. Similarly, some parasites seem to rely on shape to identify their host (Pinero et al. 2006). Furthermore, the shape component of sexual signals possibly influences both inter-specific and intra-specific mate recognition. For instance, the wing patterns of some Lycaenid butterflies serve as a species-recognition signal (e.g. Fordyce et al. 2002), whereas the high levels of variation observed in ornamentally shaped birds' tails relative to other tails suggest that their evolution has been driven mainly by sexual selection (Gregoire et al. 2007). Taken together, these observations suggest that patterns of shape variation in animal signals can contain important information for receivers.

Yet, patterns of signal shape variation have rarely been investigated at the individual scale. Even in well-studied signals, such as birds' tails, most research has focussed on simple metrics of signal size, such as length and area (e.g. tail length, Møller 1994; Møller and Tegelström 1997; Bro-Jørgensen et al. 2007). Similarly, in other well-studied sexual signals, such as the colour spots of guppies, the area, saturation and contrast of colours have been explored (Endler 1995; Grether 2000; Brooks and Endler 2001) but not shape. Such a gap appears particularly significant in the context of recent hypotheses regarding complex signals. These comprise multiple components, which may interact with each other to alter a receiver's response (Hasson 1989;

Guilford and Dawkins 1993), suggesting that all the various dimensions of a signal may influence its overall significance (reviewed in Rowe 1999; Candolin 2003; Hebets and Papaj 2005).

An obvious reason for the lack of empirical studies of ornament shape is the technical challenge of measuring shape in a meaningful way. The purpose of this study is thus to introduce a novel method to quantify the shape of animal signals. We illustrate its ease of use and potentialities, especially regarding the analysis of inter-individual variation, by directly applying it to a classic example in the field of sexual signals: primate sexual swellings.

Exaggerated sexual swellings are complex signals produced by oestrous females of many catarrhine primate species. During each oestrous cycle, the anogenital skin gradually swells, reaching its maximal size around the time of ovulation, before rapidly returning to its non-swollen state. In baboons for instance, this swollen period lasts 15–20 days in an oestrous cycle of about 35 days in length (Wildt et al. 1977). Associated changes also occur in the shape, turgidity, and colour of the anogenital skin, and female behaviour becomes sexually receptive (Rowell 1972; Dixson 1983). Comparative studies have shown that swellings evolved independently at least three times in the catarrhine lineage (Dixson 1983; Nunn 1999) and are associated with specific aspects of the mating system (Clutton-Brock and Harvey 1976; Pagel and Meade 2006), but there is no current consensus on their evolutionary significance. Most hypotheses proposed to date account for the evolution of the swelling as an indicator of ovulation, and thus as a 'within-females' signal (e.g. Clutton-Brock and Harvey 1976; Hrdy 1981; Hamilton 1984; Nunn 1999). Nevertheless, it is also possible that these signals might convey further information as a 'between-females' signal, for instance with respect to the bearer's species or individual characteristics (Pagel 1994).

Our analysis focuses on two primate species, chacma baboons (*P. ursinus*) and mandrills (*M. sphinx*), which show a similar morphological pattern of sexual skin with a pronounced swelling of the clitoridal skin, the vulval area and the entire circumanal region (Dixson 1983). Using a mathematical method developed in morphometry we first build quantitative estimators of the two-dimensional shape of the sexual swellings. We then use these estimators to ask four questions: (1) Is shape a species-specific characteristic? (2) Does shape vary within females (across oestrous cycles) and between females? (3) Are swelling size and shape correlated across individuals? (4) Are individual traits associated with shape? Finally, using the quantitative shape estimators, we assess whether the differences in shape found between females within the two species are visually detectable by a series of experimental trials using human judges.

Materials and methods

Study subjects and photographs

Chacma baboons were studied in a wild desert population at Tsaobis Leopard Park in Namibia, while captive mandrills housed socially in large enclosures were observed at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon. Background information on both sites and populations can be found in Cowlishaw (1999) and Setchell (1999), respectively. Data were collected from 15 female baboons over one to three cycles from two habituated troops (troops L and J, containing 32 and 57 individuals, respectively) during two consecutive field seasons (July–December 2005, May 2006–January 2007), producing a total of 27 cycles. For mandrills, data were collected from 18 females over one to two cycles from two enclosures (containing approximately 50 and 120 individuals) during three consecutive mating seasons (June–November 2002–2004), also producing a total of 27 cycles. In both populations, daily records were kept of the swelling status of all females, allowing determination of the peri-ovulatory phase of the cycle. This is the 5-day period before swelling deturgescence, when ovulation is most likely and when swellings achieve their maximal size (Wildt et al. 1977; Shaikh et al. 1982).

Our shape data were extracted from high-resolution photographs of maximal swellings taken opportunistically throughout the peri-ovulatory period. The pictures were taken by the same photographer (within a given species), when the animal was standing with its four feet on the ground (to minimise biases introduced by the swelling angle to verticality, ϕ) and from directly behind the animal (to minimise biases introduced by the swelling angle to the right or left, θ; see Fig. S1 in the Electronic supplementary materials). Although it was not possible to ensure that the angles ϕ and θ were always 90° exactly, the variation in these angles between images was minimal and without any consistent bias. Swelling rotation within the plane parallel to the camera objective does not influence subsequent shape analyses (details on image standardisation are provided below). For baboons, in order to quantify swelling size (area) from the same pictures, the distance separating the monkey from the photographer was measured using a rangefinder (Bushnell) with 1-m accuracy.

Quantifying the size and shape of sexual swellings

Suitable images, i.e. images showing no disrupting angles and where the tail was not masking part of the swelling, were processed. Five images per cycle were available for each baboon and one image per cycle for each mandrill. The closed two-dimensional contour of the swelling (i.e. swelling shape) was manually extracted using a semi-automatic image processor implemented in Matlab 7.0. These contours were then used to determine swelling size and shape. In the first case, swelling size was estimated as the area within the two-dimensional contour. In the mandrills, the area of the swelling contour was calculated for 17 females (26 cycles) using corresponding swelling length values taken from Setchell and Wickings (2004). In the baboons, the area of the swelling contour was calculated for 14 females (24 cycles). In the case of 11 baboons (21 cycles), swelling area was estimated by counting the number of pixels within the contour, where pixel size was determined by a calibration equation with baboon–photographer distance empirically established for the camera using a constant zoom (for further details see Caillaud et al. 2007). The capture of both baboon troops during the study (see below) also allowed us to estimate swelling area for a further three females (three cycles), where swelling area was scaled from the image using direct measurements of tail width and callosities. During the troop captures, we also validated both estimation methods by comparison with direct measurements of the swelling sizes of four captured females. This validation demonstrated that the image-based estimates of swelling area were robust, ranging within 7% of direct swelling measurements.

To quantify swelling shape, the swelling contours were imported into the SHAPE ver. 1.3 software (Iwata and Ukai 2002), freely available at http://cse.naro.affrc.go.jp/iwatah/shape/. This software automatically describes the contours by a chain code (Freeman 1974), meaning that the contour is represented as a counter-clockwise sequence of x and y coordinates of ordered points starting at an arbitrary point of the contour. The coefficients of EFDs were then calculated by the discrete Fourier transformation of the chain-coded contour through the procedure proposed by Kuhl and Giardina (1982). This method, which can be used to delineate any two-dimensional contour and is implemented in the SHAPE software (Iwata and Ukai 2002), is described below and illustrated in Fig. 1. If the distance between the $(i-1)$th and the ith chain-coded points is denoted Δt_i, the distance from the starting point to the pth point is $t_p = \sum_{i=1}^{p} \Delta t_i$, and the perimeter of the contour is $T = t_K$, where K is the total number of the chain-coded points of the contour. Given that the contour is closed, the Kth point is equivalent to the starting point. The x and y coordinates of the pth point are thus $x_p = \sum_{i=1}^{p} \Delta x_i$ and $y_p = \sum_{i=1}^{p} \Delta y_i$, where Δx_i and Δy_i are the distances along the x- and y-axes between the $(i-1)$th and the ith points of the contour. Then, the elliptic Fourier equations giving the coordinates x_p and y_p on the contour are

$$x_p = A_0 + \sum_{n=1}^{\infty} \left(a_n \cos \frac{2n\pi t_p}{T} + b_n \sin \frac{2n\pi t_p}{T} \right)$$

and $y_p = C_0 + \sum_{n=1}^{\infty} \left(c_n \cos \frac{2n\pi t_p}{T} + d_n \sin \frac{2n\pi t_p}{T} \right)$; (A_0/C_0) are the coordinates of the central point and n is the harmonic
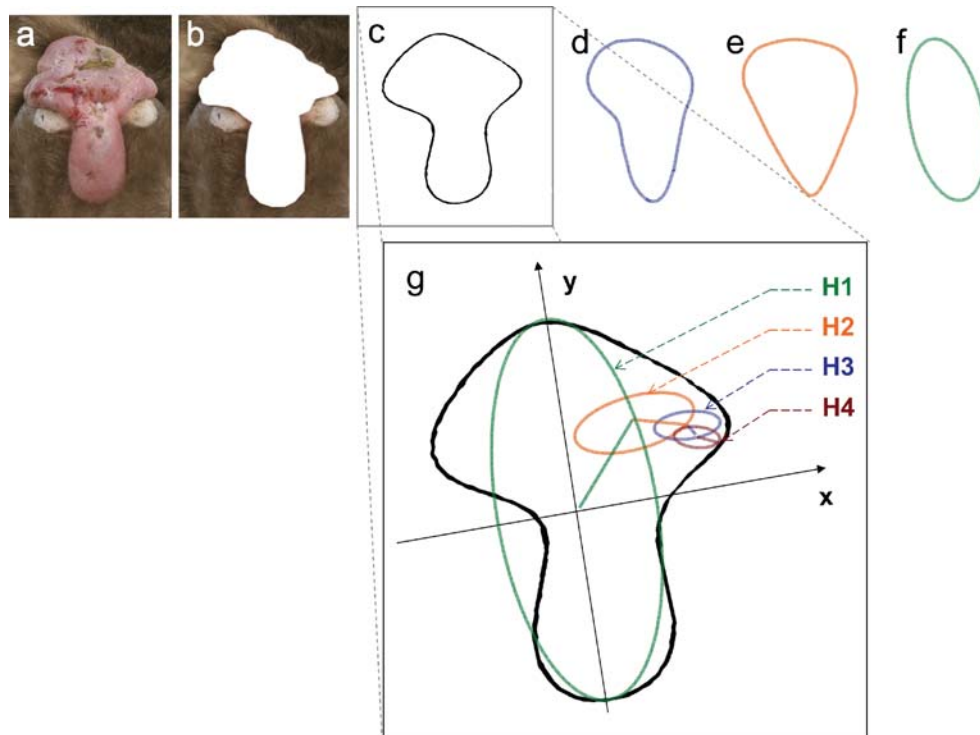
Fig. 1 Extraction and analysis of a swelling contour using elliptic Fourier descriptors. **a** Original photograph of a swelling. **b** Extraction of the two-dimensional contour of the swelling. **c** Decomposition of the same contour by elliptic Fourier descriptors (EFDs) using four harmonics, **d** using three harmonics, **e** using two harmonics, and **f** using only the first harmonic. **g** Illustration of the principle of EFDs. The harmonic of rank n is designated by Hn. The harmonic of rank $n+$ 1 moves around the Hn orbit. The more harmonics are added, the more closely the reconstructed outline converges onto the original outline. The longest axis of the swelling (y-axis) designates the starting point (highest point of the swelling). The outline is then described by a mathematical function, which measures the distance of the starting point to a given point on the outline

order. a_n, b_n, c_n and d_n are the four elliptic Fourier coefficients of the nth harmonic. a_n and b_n are given as:

$$a_n = \frac{T}{2n^2\pi^2} \sum_{p=1}^{K} \frac{\Delta x_p}{\Delta t_p} \left(\cos\frac{2n\pi t_p}{T} - \cos\frac{2n\pi t_p - 1}{T} \right)$$

$$b_n = \frac{T}{2n^2\pi^2} \sum_{p=1}^{K} \frac{\Delta x_p}{\Delta t_p} \left(\sin\frac{2n\pi t_p}{T} - \sin\frac{2n\pi t_p - 1}{T} \right)$$

The coefficients of the y coordinates, c_n and d_n, are found in the same way.

The resulting coefficients are subsequently normalised to be invariant with respect to the size, rotation and starting point (Iwata and Ukai 2002), with the procedure based on the ellipse of the first harmonic where the size, orientation and starting point of the contour is standardised in accordance with the size and alignment of the major axis of the ellipse (see Kuhl and Giardina 1982 for a detailed description of this procedure). This normalisation means that the quantification of swelling shape using the Fourier method is independent both from swelling area (and monkey-to-photographer distance, since the photograph resolution was high within the full range of distances considered) and from swelling orientation within the two-dimensional plane. In the present study, swelling shape was approximated by the first four harmonics (see Fig. S2 in the Electronic supplementary materials for additional details regarding the number of harmonics to be used in shape description). Thus, 16 coefficients (four harmonics each described by four coefficients) were derived from the swelling contour.

Normalised Fourier coefficients cannot be used as direct shape characteristics because the number of coefficients is large, and the morphological meaning of each is difficult to interpret separately. Such information is thus more usefully summarised using a principal components analysis (PCA) based on a variance–covariance matrix that is directly carried out on the Fourier coefficients (Rohlf and Archie 1984). Following this procedure on the baboon and mandrill coefficients, the first principal component was then adopted as our quantitative shape estimator for each sexual swelling. A minor part of the variance in swelling shape was explained by the second and third principal components (see Results), so subsequent analyses using the second and third principal components as the quantitative shape estimator are also presented in the Electronic supplementary materials.

To investigate whether swelling shape was a species characteristic, a PCA was first conducted on both species together. Since we have repeated observations ($n=5$) for each baboon cycle but not for mandrill cycles, we selected one data point among these observations for baboons, using the median of the shape estimator values, to keep the number of observations comparable between the two species. To investigate inter-individual shape variations within species, a PCA was subsequently conducted on the Fourier coefficients for each species separately.

Assessment of swelling shape by human judges

For a subset of baboon and mandrill cases, where the shapes of two cycles per female were available ($N=9$ in both species), we reconstructed each swelling contour from the calculated Fourier coefficients by the inverse Fourier transformation (Furuta et al. 1995). This standardised all swelling contours for size and resolution. Eighty human judges (40 women and 40 men) were then recruited voluntarily among students of the University of Montpellier to analyse whether between-female variation in swelling contour was detectable despite within-female variation across consecutive cycles. Specifically, we asked them to identify the swelling contours that corresponded to two different cycles of the same female. The judges were presented with the swelling shape of the focal female alongside three other contours: the shape of another cycle from the same female and two other shapes belonging to two different females of the same species. A computer program (written in Delphi, version 7, see Alvergne et al. 2007) was used to present the contours, randomising the presentation and order of females within species and whether a test started with mandrills or baboons. Each shape was seen once by each judge. The similarity between cycles of a given female was expressed as the proportion of correct assignments from all judges. Thus, the expected value varies between 1/3 (no similarity) and 1 (perfect similarity).

Individual traits

The influences of age, body condition, parity (mandrills only) and dominance rank on swelling shape were also investigated. To determine age and condition in the baboons, 14 of the 15 females were captured and anaesthetised within 6 months of cycling. Briefly, troops were captured using individual cages baited with corn cobs and set up at dusk. The baboons were captured at dawn, anaesthetised using tiletamine–zolazepam and all processed within a day, in order to be released together the following morning when fully awake. While the baboons were anaesthetised, age was estimated through dentition. Tooth eruption schedules for wild baboons (Kahumbu and Eley 1991) were used to age animals until they acquired a full set of teeth. Beyond this point, age was estimated using molar wear rates, calculated by matching observed patterns of wear to the known time elapsed between the eruptions of the first, second and third molars. Subsequent validation of this approach, using individuals that had been captured on multiple occasions for a comparison of estimated versus known age differences between captures, indicates that these estimates were robust (Cowlishaw, unpublished data). Female body mass and crown-rump length were also measured at this time. For mandrills, age and parity (number of births per female) were determined from management records. All mandrills were also captured and anaesthetised for an annual health check within 3 months of cycling, at which time individuals were also weighed and their crown-rump length determined (Setchell and Wickings 2004). In both species, individual condition was scored according to a standard body mass index, calculated as mass/length^2. The choice of this index was guided by previous work carried out on swellings in the mandrill population (Setchell and Wickings 2004) and in other populations (e.g. Emery and Whitten 2003) for comparative purposes.

To determine individual dominance rank in the baboons, agonistic and approach–avoid interactions were collected using ad libitum and focal observations across the study period. Dominance rank calculations indicated a high degree of linearity in both study troops using Landau's linearity index corrected for unknown relationships (h') (de Vries 1995) and tested by a χ^2 test (Appleby 1983): $h'=0.95$, $\chi^2=63.63$, $df=20$, $P<0.001$ for troop L, and $h'=0.67$, $\chi^2=93.55$, $df=25$, $P<0.001$ for troop J. Similarly, in the mandrills, ad libitum records of agonistic and approach–avoid interactions between females during observation periods were used to confirm previous records of dominance rank established in 1996-1997 (for further details, see Setchell 1999). These data indicated that there have been no changes in relative female ranks in the mandrill colony, with the exception of births and deaths, since 1996 (Setchell, unpublished data). In order to control for differences in troop size, a female's rank is expressed as the percentage of the group's adult females ranking below her.

Statistical analyses

Three sets of generalised linear mixed-effect models (GLMMs) were carried out, using the swelling shape estimator (i.e. the first component of our PCA analyses) as the response variable in each case. A mixed-model approach controls for the occurrence of repeated measures within levels of a given factor if this factor is treated as a random effect (Pinheiro and Bates 2000). The first model

was designed to investigate whether shape is a species characteristic; thus, 'species' was treated as a fixed categorical factor, whereas 'female identity' was treated as a random effect to control for the potential occurrence of multiple measures (due to multiple cycles) per female. The second set of models was designed to investigate whether shape is an individual characteristic and involved one model for each species. Using the baboon data, we analysed those baboons in which repeated shape estimations per cycle were available for each female and adopted a hierarchical random effects structure, entering 'cycle identity' nested within 'female identity' nested within 'group identity'. For the mandrill data, repeated observations per cycle were not available (see "Quantifying the size and shape of sexual swellings", above); therefore, only 'female identity' and 'group identity' were entered as random effects. This approach allowed us to estimate the proportion of the variance accounted for by each random effect, i.e. whether variation was seen within individuals (for baboons), between individuals (for baboons and mandrills) or between groups (for baboons and mandrills). The third set of models were designed to investigate whether measured individual traits—namely age, dominance rank and body condition—were associated with shape. This was achieved by the addition of these individual traits as fixed factors to the second GLMM described above. None of these fixed effects were significantly correlated in either species, and the random effects structure from the second set of models was preserved. In mandrills, swelling shape scores were better fitted using a non-linear relationship with age: Akaike Information Criterion (Akaike 1974) values were −57.1 for the model using $\log_e$-transformed data and −52.4 for the linear model. In baboons, both models performed equally well (AIC value of −572.1 for the linear model and of −571.9 for the $\log_e$-transformed data). On this basis, the age data were $\log_e$-transformed for both species for comparative purposes. In addition, since our age estimates for baboons were based on dentition (and thus may be less precise than for mandrills), we conducted a non-parametric Spearman correlation test (treating ages as ordinal data rather than interval data) to confirm the GLMM results. For mandrills, data on parity were also available. However, parity and age were highly correlated in the sample (Spearman correlation test, rho= 0.95, $n=17$, $P<0.01$), so it was not possible to introduce both variables into the same model to disentangle their effects.

In each GLMM, the significance of a random effect was tested by performing likelihood ratio tests (following a χ^2 distribution) comparing two models differing only in the presence of this effect, while the significance of fixed effects was evaluated using F-Wald tests (Pinheiro and Bates 2000). Statistical significance is reported for

non-simplified models (i.e. full models) throughout (Whittingham et al. 2006). In addition, since the first principal component of the PCAs did not explain all the shape variation, all the models presented above were also run using the second and third principal components (instead of the first) as the swelling shape estimator (see the Electronic supplementary materials for the results of these latter analyses).

To investigate whether swelling size and shape were correlated, swelling size and shape scores were averaged for each female and correlated across females of the same species using a Spearman rank correlation test.

To analyse how well human judges assessed female identity using their swelling shape in our experimental trials, the statistical significance of correct assignments was estimated for both species using exact binomial tests. Thus, the response variable was 0 in the case of incorrect assignments (the judge did not recognise two shapes as belonging to the same female) and 1 in the case of correct assignments (the judge did recognise two shapes as belonging to the same female). We then tested for differences in between-cycle similarity between the two species using a binomial mixed model, with species as a fixed effect and both judge and female identities as crossed random effects. The significance of the fixed factor (species) was evaluated using a χ^2 test (non-linear mixed model). The mixed model also allowed us to perform a posteriori contrasts on species to avoid pseudoreplication when testing the difference between the mean rate of correct swelling assignments for the two pooled species and the rate expected by chance. For a posteriori contrasts, P values were calculated using a sample generated after 10,000 simulations from the posterior distribution of the parameters of the fitted model using Markov chain Monte Carlo methods (Bates and Sarkar 2007).

All statistical analyses were run using the R software version 2.5.1 (The R development core team, http://www.r-project.org/).

Results

Is swelling shape a species characteristic?

Fourier coefficients of mandrill and baboon swelling contours were analysed together in a PCA to see if swelling shape differs between species (or at the genus level). The proportion of the total shape variation accounted for by the first and second principal components was 58% and 20%, respectively (Fig. 2). Analysis of the shape estimator (the first principal component) indicates that swelling shape significantly differed among species ($F_{1,31}=62.5$, $P<0.001$).
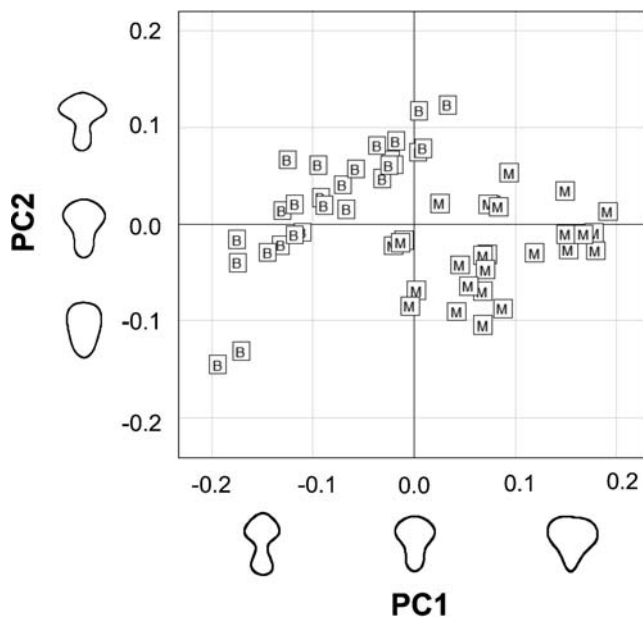
Fig. 2 PCA results on Fourier coefficients describing the swelling contour for 27 baboon cycles ($N=15$ females) and 27 mandrill cycles ($N=18$ females). This plot shows the cloud of swelling contours on the first two axes of the interspecific PCA, respectively labelled PC1 and PC2. To help visualisation, the variation in swelling shape accounted for by PC1 and PC2 is illustrated on the relevant axis using the inverse Fourier transformation. In each case, middle shapes are reconstructed by letting the score on a particular component be equal to the sample mean (±2 standard deviations for top and bottom shapes), while the scores on the remaining components remained at the sample mean. Baboons and mandrills are respectively labelled 'B' and 'M'

Is shape an individual characteristic?

The baboon shape estimator, i.e. the first principal component extracted from the baboon Fourier coefficients (15 females and 27 cycles), accounted for 56% of the variance in shape (Fig. 3a). Analysis of the random effects of 'group', 'female' and 'cycle' on swelling shape revealed no significant differences between troops ($\chi^2=0.22$, $df=1$, $P=0.64$) but significant differences between females ($\chi^2=308.54$, $df=1$, $P<0.001$) and between cycles of a given female ($\chi^2=52.04$, $df=1$, $P<0.001$). The proportion of variance explained by 'female' and 'cycle' in the model were 64% and 20%, respectively. These results indicate that swelling shape differs consistently between as well as within female baboons.

The mandrill shape estimator, i.e. the first principal component extracted from the mandrill Fourier coefficients (18 females and 27 cycles), accounted for 60% of the variance in shape (Fig. 3b). The analysis of group effects on the shape estimator was not significant ($\chi^2=0.68$, $df=1$, $P=0.41$). There were significant differences in swelling shape between females ($\chi^2=12.41$, $df=1$, $P<0.001$), and the 'female' effect explained 72% of the total variance in the

model. These results indicate that swelling shape also differs consistently between mandrill females.

Are swelling size and shape correlated across females?

There was no correlation between swelling area and shape scores across individuals in either baboons (Spearman's correlation, rho$=-0.23$, $n=14$, $P=0.43$) or mandrills (rho$=0.21$, $n=17$, $P=0.42$).

Are individual traits associated with swelling shape?

In baboons, swelling shape displayed a significant non-linear relationship with age ($F_{1,9}=26.90$, $P<0.001$, Fig. 4a) but not with dominance rank ($F_{1,9}=4.09$, $P=0.07$) or body condition ($F_{1,9}=0.97$, $P=0.35$) using a GLMM. The age pattern was confirmed using a non-parametric correlation linking age (fitted as ordinal rather than interval data) and average swelling shape score across individuals (rho$=-0.82$, $n=14$, $P<0.001$). The relationship was still significant (rho$=-0.84$, $n=13$, $P<0.001$) when removing a female, which appeared as an outlier to the regression line
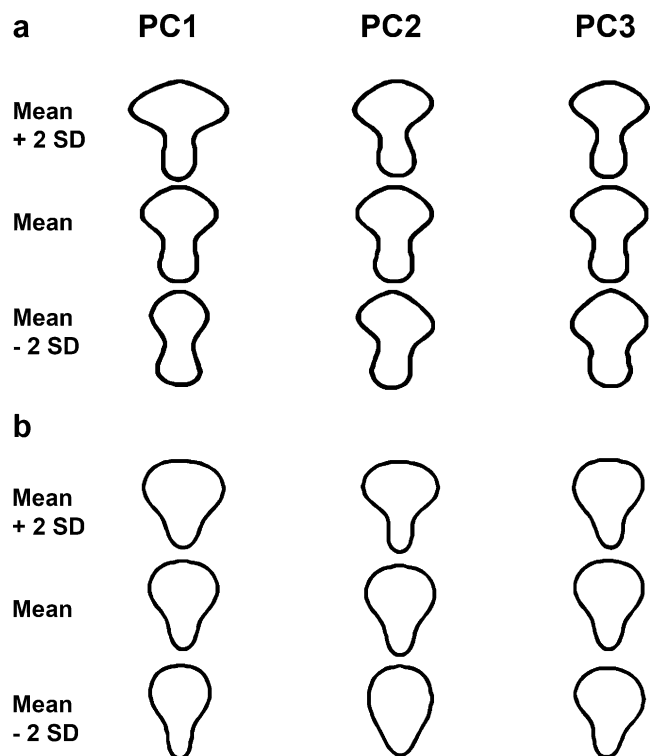

Fig. 3 Visualisation of swelling shape variation in baboons (**a**) and mandrills (**b**) accounted for by the first three components of the Fourier coefficients PCA. For each principal component (PC), the *mean outline* represents the shape reconstructed using the mean score in the sample, and the *top and bottom shapes* represent the shapes reconstructed using mean score ±2 standard deviations. Scores on the remaining components remained at the sample mean
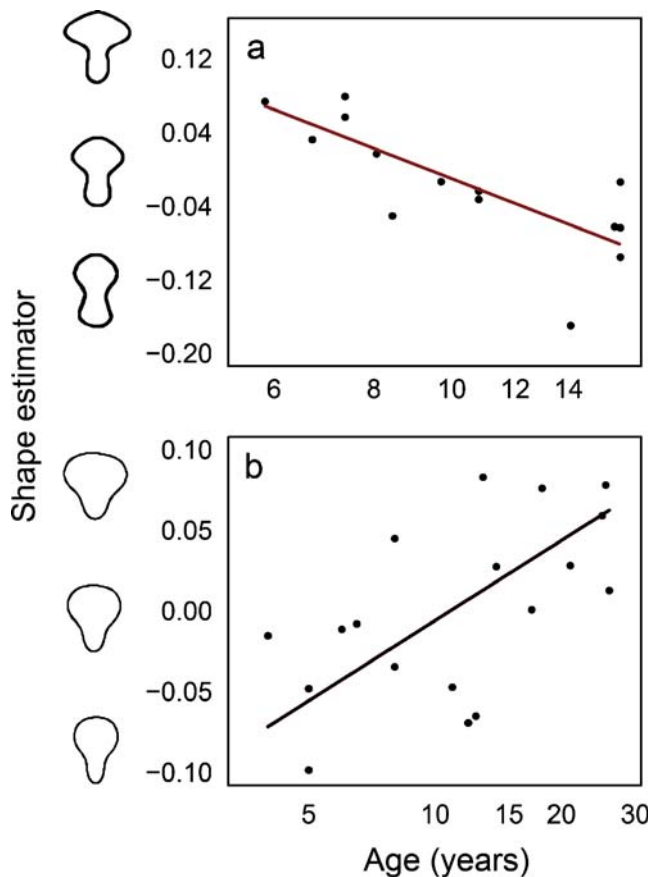
Fig. 4 Relationships between swelling shape and age in baboons (**a**) and mandrills (**b**). The *line* indicates the fitted values for age (plotted on a log axis), calculated using the parameter estimates of the GLMM. To help visualisation, the variation in swelling shape accounted for by PC1 is illustrated on the relevant axis using the inverse Fourier transformation. *Black dots* represent individual means

(see Fig. 4a). According to this result, young female baboons exhibited high positive scores for swelling shape. This indicates that the top of the swelling is wide in youth relative to the basal apex, but the top becomes narrower and the basal apex broader with age.

Similarly, mandrill swelling shape displayed a significant non-linear relationship with age ($F_{1,6}=9.10$, $P=0.02$, Fig. 4b) but not with dominance rank ($F_{1,6}=1.05$, $P=0.35$) or condition ($F_{1,6}=1.24$, $P=0.31$). Here, the swelling shape is elongated along its vertical axis in youth but becomes increasingly squat with age. Parity, when added into the previous mandrill model instead of age, also showed a significant relationship with swelling shape score ($F_{1,6}=13.92$, $P<0.01$).

Is shape variation visually detectable?

When human judges were asked to identify swelling shapes from different cycles of the same female, their success rates

were 0.64 for baboons and 0.66 for mandrills, significantly higher than the 1/3 expected by chance (exact binomial test; baboons, $P<0.001$; mandrills, $P<0.001$). When controlling for pseudoreplication using a mixed model, the reported consistency in shape between consecutive cycles of the same female remained (binomial mixed model: simulated P value, $P<0.001$), and judges performed equally well in both species ($\chi^2=0.14$, $df=1$, $P=0.70$). These results suggest that the quantitative shape estimators capture visually detectable patterns.

Discussion

The sexual ornamentation of animals is a classical theme in studies of sexual selection. However, while patterns of size variation in sexual signals have been widely studied, shape variation has been largely neglected. In the present study, we have introduced a novel technique for the measurement of shape in such signals. The potential power of this approach is demonstrated in our analysis of catarrhine anogenital swellings. Here, we have found that patterns of shape variation reflect consistent differences both between species (or genera) and between individuals, with the latter showing similar associations of shape with age in both taxa.

Our quantitative measure of swelling shape derives from elliptical Fourier descriptors (EFDs). Such descriptors have been previously proven as suitable for the evaluation of a wide range of biological shapes such as fruits, petals and shells (Rohlf and Archie 1984; Currie et al. 2000; Tort 2003; Yoshioka et al. 2004). To our knowledge, this is their first application in a study of sexual signals. Moreover, whereas previous biological studies using EFDs have been largely descriptive, our study illustrates the potentialities of this method by subsequently analysing patterns of shape variation at various scales: not only among species but also between and within individuals. Nevertheless, we have not explored such potentialities in an exhaustive way, since EFDs may prove useful to investigate other important issues in behavioural ecology, for instance relative to the study of symmetry (see Iwata et al. 1998; Yoshioka et al. 2004 for an illustration of the possibilities of EFDs in this particular context). While shape quantification through EFDs in wild animal populations inevitably involves methodological challenges, in this case, the use of field photographs (where slight angle variations between pictures might potentially add noise to the data and reduce analytical power), our results indicate that clear and consistent patterns are still detectable under field conditions—both within and between species. Finally, using EFDs allows useful flexibility in the analytical resolution of shape description. Thus, depending on the needs of the analysis, one might choose to include higher order harmonics to

capture fine-grained shape variations, or alternatively, exclude them as a way of removing part of the measurement error (Claude 2008). Overall, EFDs appear to be a powerful and sensitive solution to the quantitative investigation of shape in behavioural ecology.

In this study, we have also compared the performance of EFDs with a very different method of analysing between- and within-individual shape variations in swelling contour, namely a qualitative technique involving human judges. Similar results were obtained in both cases, suggesting that the quantitative shape estimators are robust. Moreover, baboons and mandrills, like humans, are Old World primates and have a very similar visual system to our own (Jacobs 1993; van Essen and Anderson 1995). Therefore, the comparability of the results obtained through both methods suggests that the shape variation captured by EFDs provides biologically meaningful information, i.e. information that is likely to be detectable by conspecifics.

The global pattern of morphological variation in primate sexual swellings (including the anatomical distribution, coloration and oedema of the sexual skin) across species remains poorly understood. Nevertheless, swelling morphology has sometimes been suggested to act as a barrier to cross-species fertilisation in some cercopithecine lineages (Dixson 1983). We focused on two related species that exhibit the same anatomical distribution of sexual skin, yet found quantitative evidence of intergeneric divergence in the shape of these female sexual ornaments. According to a traditional view of mating signal evolution, certain features of the mating signal serve for species recognition whereas a different set of components is used to make intra-specific mating decisions. This may be true for many multivariate signals (Pfennig 1998) and implies that mate choice operates as a two-step process. In the first step, a decision is made about species identity; the second step then involves a decision about mate quality. According to this framework, strong directional selection often shapes the evolution of signal properties involved in intra-specific mate choice (reviewed in Andersson 1994). This in turn often leads to exaggerated morphological features such as the long eye stalks of diopsid flies (Cotton et al. 2004), the brightly coloured plumage of some birds (e.g. Norris 1993) or possibly the large sexual swellings of some primates (Pagel 1994; Domb and Pagel 2001). In contrast, stochasticity in selective pressures may lead to high levels of raw diversity in some other traits, which may then favour their evolution as reliable species indicators, such as bird tail shape (Gregoire et al. 2007), butterfly wing pattern (Fordyce et al. 2002) or perhaps primate swelling shape.

Following this hypothesis, and given that swelling size and shape scores are statistically independent, it is possible that these different morphological aspects of the swelling are used in different contexts. Swelling size, which

correlates with ovulation probability (chimpanzees, Emery and Whitten 2003; Deschner et al. 2004; baboons, Gesquiere et al. 2007; Higham et al. 2008) influences intra-specific male mate choice in many primates, as shown by experimental studies (Bielert and Anderson 1985) and in wild populations (chimpanzees, Deschner et al. 2004; baboons, Gesquiere et al. 2007). Swelling shape, which apparently differs between species, may possibly serve (or may have served in the past) for species recognition in inter-populational or inter-specific contact areas. Future studies might usefully compare the extent of swelling shape variation between closely related species where interbreeding occurs, e.g. at the hybrid zone between the olive baboon *Papio anubis* and hamadryas baboon *Papio hamadryas* in Ethiopia (Nagel 1973; Phillips-Conroy and Jolly 1986). Shape variation between such species at hybrid zones may be lower than between sympatric species where interbreeding does not occur.

However, an alternative and perhaps more realistic view of mate choice proposes that all mating preferences, even those at the species level, evolve as a direct consequence of selection of the 'best' mate among the available choices (Ptacek 2000). Accordingly, being a conspecific is one important aspect of being the best mate, but the process of mate choice is the same at all levels of discrimination (both intraspecific and interspecific), thus making species recognition a consequence of finding the best mate (Littlejohn 1999). In this context, divergence in the species-recognition properties of mating signals may merely be an epiphenomenon of (or at least evolve jointly with) intraspecific sexual selection (Gerhardt 1982).

In our case, this would suggest that sexual swelling shape might influence intra-specific mate choice as well as inter-specific mate recognition. Swelling shape was found to be more variable between females than across consecutive cycles of the same female. As such, it is possible that shape conveys information about individual characteristics. Among the variables tested in this study, shape was found to co-vary with female age. The precise pattern of co-variation between the shape estimator and age differed between species, possibly as a consequence of inter-specific divergence in mate choice criteria, with the relative width of the top part of the swelling decreasing with age in baboons but increasing with age in mandrills. Nevertheless, a general pattern appeared to be that the width of the basal apex of the swelling, relative to its top, was narrow in youth and became broader with age (see Fig. 4). Given these patterns of association, to what extent might individual variation in swelling shape reflect female 'quality' from a male perspective?

Among primates, older, multiparous females have higher reproductive success than younger, nulliparous and primiparous females (reviewed in Anderson 1986). Such females

are not only more fertile, exhibiting shorter inter-birth intervals (baboons, Strum and Western 1982; Smuts and Nicholson 1989; Wasser et al. 1998; Altmann and Alberts 2003; mandrills, Setchell et al. 2002) but also experience higher infant survival rates (baboons, Altmann 1980; Smuts and Nicholson 1989; Wasser et al. 1998) and produce larger offspring (baboons, Johnson 2003; mandrills: Setchell et al. 2001). Thus, by changing with age, shape may convey potentially useful information about fertility and infant survival. Alternatively, the age–shape relationship may reflect co-variation with parity (number of births) rather than fertility. Age and parity were strongly correlated in this mandrill sample but may show weaker correlations in wild primate populations. Swelling shape may thus indicate past reproductive success, which in turn might reflect female quality (since higher quality females will produce more offspring). Whether it would be more useful for a female to advertise current fertility or historical reproductive output remains an open question, but the two hypotheses are not mutually exclusive.

Should males use the age-associated patterns of shape variation when making mating decisions? The associations between age, fertility and parity indicate that males should benefit from preferring older females, and in line with this expectation, such a preference is one of the most consistently reported criteria for mate choice in male primates (Anderson 1986; Paul 2002; Muller et al. 2006). Similarly, males prefer parous females in mandrills (Setchell and Wickings 2006). Alternative morphological cues of age, such as body size and nipple elongation, are also available (Altmann et al. 1981). However, such indices may be less precise and less obvious than swelling shape, especially from a distance. This may be particularly important for dispersing males who have left their natal troop and are seeking to immigrate into a troop that maximises their reproductive opportunities (Alberts and Altmann 1995). Females in turn benefit from attracting such males to enter the troop when they are in oestrus, since a later arrival by the same male might otherwise lead to infanticidal attacks and the death of their infant (van Schaik et al. 2004). Unsurprisingly, given these selection pressures, the age-related expression of sexual signals in female primates may be widespread. For example, in female geladas *Theropithecus gelada*, changes in the sexual skin (i.e. changes in the colour, quality and dispersion of the fluid-filled vesicles that border the female's chest during oestrus) have been shown to be age-dependent (Dunbar 1977). Similarly, age, parity or both influence swelling size in several species (reviewed by Anderson and Bielert 1994), where the swellings of adolescent or nulliparous females relative to those of adult or multiparous females are either larger (chimpanzees, Emery and Whitten 2003; olive baboons, Higham et al. 2008) or smaller (mandrills, Setchell and Wickings 2004; yellow baboons, Gesquiere et al. 2007).

If swelling size can indicate age group or reproductive group, does swelling shape convey independent or redundant information? Given that swelling size and shape are not correlated, they may be linked to age or parity by different relationships. For instance, in the same mandrill sample used here, a previous study found that nulliparous females displayed smaller swellings than multiparous females, but in contrast to swelling shape, there was no relationship linking swelling size to age (Setchell and Wickings 2004). Thus, males, by considering swelling shape in addition to swelling size, may obtain more accurate information on female age. This conclusion emphasises that the study of the signal in its entirety, taking into account its various components such as swelling size, shape and even colour, may be necessary to fully understand its significance.

Overall, our study suggests that it is possible to measure shape in sexual signals and that, in the case of primate sexual swellings, shape may play a role in both species recognition and the signalling of individual characteristics. This opens two immediate perspectives for the future. First, in the context of sexual swellings, experimental studies have shown that supernormal-sized swellings elicit greater male sexual arousal than normal-sized swellings (Bielert and Anderson 1985). Investigating male response to swelling shape variation using the same type of protocols should help our understanding of whether male primates use swelling shape when making mating or dispersal decisions. Second, more generally, this research opens a new avenue to studying two-dimensional shape in behavioural ecology across a variety of species and signalling systems. Future research adopting the methods used in this study should help us to build a wider picture of the evolution and maintenance of the shape component in animal signals.

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