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Agonistic screams differ among four species of macaques: the significance of motivation-structural rules

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We compared screams of four species of macaques (rhesus monkey, *Macaca mulatta*; pigtailed monkey, *M. nemestrina*; Sulawesi crested black macaque, *M. nigra*; stumptailed macaque, *M. arctoides*) with respect to predictions of Morton's motivation-structural rules (Morton 1977, *American Naturalist*, **111,** 855–869). We examined screams produced by victims of attack that involved contact aggression (pulling, pushing, slapping, grappling and biting) from a higher-ranking opponent. For each macaque species, we digitized 100 screams from females 3 years of age or older and measured acoustic features of each call. We used discriminant function analysis to determine whether the 400 vocalizations could be assigned to the correct caller species on the basis of their acoustic structure. Calls were assigned to the correct species at a significantly higher rate (93.5%) than expected by chance (25%). Each of the four macaque species used acoustically distinct screams in a shared context. While the differences in the macaque species' vocalizations suggest no simple correlation between immediate context and the acoustic forms of screams, there was general correspondence between the acoustic structure predicted by motivation-structural rules and inferences about the internal state of the vocalizer derived from the typical intensity of aggressive patterns that characterize each of the four species.

Identification of the factors involved in the evolution of signal design and form is critical in animal communication research. Ecological and biological conditions that have had significant impact on the physical nature of signals include: the distance over which communication must be effective, the energetic costs of communicating, body size and structure, physical properties of the habitat, the timing of communication, the number and phylogenetic relationships of sympatric species, the presence and behaviour of both conspecific competitors and those of other species, and costs imposed by predators (reviewed in: Gerhardt 1983; Wiley 1983; Hauser 1996a; Bradbury & Vehrencamp 1998). For some of these considerations, the impact on design structure has been more significant for signals used over relatively large distances. Signal structure for shorter-distance communication will be less influenced by selection imposed by the problems of production, effective transmission and detection in natural habitats, but none the less takes forms that may be understood from an evolutionary perspective.

Evolutionary accounts of signal structure for shorter-distance communication date from Darwin's 'principle of antithesis' (Darwin 1872), which proposed that signals associated with opposing states or behaviours would undergo selection to minimize ambiguity and take antithetical forms. For vocalizations, Morton (1977, 1982) outlined a set of 'motivation-structural (MS) rules' which specify that harsh (broadband), lower-frequency vocalizations are widely used in hostile and aggressive contexts, and tonal, higher-frequency calls in appeasing or friendly situations. Morton (1977) noted that the ability to produce harsh sounds of lower frequency is linked to body size and, in many species, size determines the outcome of aggressive encounters. Thus, selection would favour the use of such vocalizations during aggressive conflict because they reflect size and can reliably replace overt fighting, with communication as the determinant of resource-holding potential, which Morton (1994) has termed 'expressive size symbolism'. Owings & Morton (1998, page 111) suggested that more complicated use of vocalizations evolved when the direct and, for the most part (see Hauser 1996a, page 479), fixed-sound symbolism of amphibian vocalizations was modified by motivational factors in warm-blooded vertebrates. Vocalizations came to reflect differences in motivation with harsh, low-frequency sounds linked to aggressive states. Appeasing, submissive or friendly vocalizations, either through selection based on the principle of antithesis or, perhaps, because of an association between the production of

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higher-pitched sounds by infants, tend to be tonal and of higher frequency. Thus, Owings & Morton (1998, page 114) pointed out that lower and harsher, or higher and more tonal, vocalizations show motivational tendencies towards opposite endpoints of expressive sound symbolism. They suggest that although states of fear and appeasement differ in motivation, they share the same symbolization of small size, which would reduce the likelihood of attack during aggressive encounters.

Owings & Morton (1998, page 115) suggested that scream vocalizations, which may occur when fear and aggression are conflicting, are both harsh and rising in frequency and usually lack species-typical attributes because they often are used between species. They contrast screams with other vocalizations that show species-typical form even though the motivation-structural code underlying them is interspecific (shared). In some species, however, screams may have been selected to serve special functions and, consequently, might show modifications of acoustic structure. Our previous work, for example, has focused on the role that macaque (*Macaca*) screams play during agonistic recruitment (Gouzoules et al. 1984, 1986; Gouzoules & Gouzoules 1989).

In several Old World monkey species combatants solicit support from other group members against opponents, employing conspicuous scream vocalizations in the recruitment process (Lindburg 1971; Cheney 1977; de Waal 1977; Gouzoules et al. 1984, 1986; Bernstein & Ehardt 1985). These vocalizations are among the loudest of the species and this can be explained if screams are directed to allies that may be some distance away, sometimes out of sight, and are not simply serving as signs of fear or submission to the attacker, as first assumed (Rowell 1962). Successful recruitment might occur because of vocal recognition of the caller and associations made between the scream and the caller's emotional state or arousal level. Another hypothesis, one that is not mutually exclusive with the above account (Scherer & Kappas 1988; Marler et al. 1992; Marler & Evans 1997), is that screams have external referents and make available more specific information about the agonistic event, information that might be of use to spatially distant allies in making decisions about intervention tactics (Gouzoules et al. 1995).

With respect to the issue of acoustic structure, Gouzoules et al. (1984) found that in rhesus monkeys, *M. mulatta*, victims of attack commonly use one of five acoustically distinct screams. Each scream type showed a statistical association with a particular class of opponent, defined in terms of relative dominance rank and matrilineal relatedness to the signaller, as well as the nature of the aggression, differentiated as to whether or not physical contact had occurred. Pigtailed macaques, *M. nemestrina*, were also found to use acoustically different screams when confronting opponents (Gouzoules & Gouzoules 1989). Although pigtailed and rhesus macaques can interbreed (Yerkes Primate Center colony records; Bernstein 1974) and have very similar patterns of social organization, the two species appear to employ acoustically different screams in essentially identical agonistic contexts. For example, during contact aggression from higher-ranking opponents, rhesus monkeys most often use broadband noisy screams, while pigtailed monkeys tend to use tonal, frequency-modulated calls. Cheney & Seyfarth (1990, page 122) and Hauser (1993, 1996a, page 478) have suggested that these observations contradict the predictions of MS rules because similar motivational states seem to be associated with different acoustic signals in closely related species.

In the present study, to extend and formalize our previous observations, we compared the scream vocalizations of four species of macaques (the rhesus monkey, the pigtailed monkey, the Sulawesi crested black macaque, *M. nigra*, and the stumptailed macaque, *M. arctoides*) for similarities and differences with respect to the predictions of Morton's MS rules. This comparison was not intended as a test of the MS rules hypothesis as such because previous studies have already provided general support for them (e.g. Morton 1977; August & Anderson 1987; Hauser 1993, 1996b). Instead, as Hauser (1996a, page 479) has noted, it is important to understand why ostensible exceptions to the predictions of MS rules arise. Thus our goal was to assess how a more formal and direct comparison of rhesus and pigtailed macaque screams, and the addition of two other macaque species to the analysis, would correspond with the MS rules hypothesis.

METHODS

Study Species

Fa (1989) reviewed the evolution and taxonomy of the genus *Macaca*, which includes 19 extant species. The four species included in the present study fall into three species groups (Fooden 1976, 1980; Delson 1980; Melnick & Kidd 1985; Hoelzer & Melnick 1996): the *fascicularis* group, which includes the rhesus monkey; the *silenus-sylvannus* group, to which the crested black macaque and pigtailed monkey belong; and the *sinica* group, to which the stumptailed macaque probably belongs, although some evidence suggests *M. arctoides* might deserve its own grouping (Hoelzer & Melnick 1996).

While all four of these species have been the subject of behavioural studies both in captivity and in the wild, the rhesus macaque has received by far the most attention and the crested black macaque the least. The four species have broadly similar social systems, with groups composed of multiple adult males and females as well as juveniles and infants (Roonwal & Mohnot 1977; Melnick & Pearl 1987; Fa & Lindburg 1996). All four species display dominance hierarchies, with position in the hierarchy determined primarily by maternal rank (Bernstein 1970; Bernstein & Gordon 1980; Bernstein & Ehardt 1985; Walters & Seyfarth 1987; de Waal 1989), and all show effects of matrilineal kinship on social behaviour patterns (reviewed in: Gouzoules & Gouzoules 1987; Bernstein 1991). Social organization, including the influence of matrilineal kinship, in the lesser-known crested black macaque has been described as similar to multimale groups in well-studied macaque species (Reed et al. 1997; Baker & Estep 1985).

Despite these overall similarities in group structure and behaviour for macaques, there are notable differences. For example, some species, such as the rhesus macaque, are seasonal breeders, while others (including *M. arctoides*, *M. nigra* and *M. nemestrina*) are not. Direct comparisons of agonistic behaviour for all (Bernstein et al. 1983) or some of the species (de Waal & Ren 1988) included in the present study have revealed differences in the frequency and specific form of aggression, and the occurrence and nature of reconciliation among macaques. Other reports have focused on agonistic behaviour comparisons between one of the species studied by us and other macaque species (e.g. Thierry 1986; Petit et al. 1997). We raise some of the findings from these studies in the Discussion.

Study Groups

The three groups of rhesus macaques ranged in size from 52 to 126 animals. The stumptailed monkey group numbered 18–26 individuals, the crested black macaque group 18–23, and the pigtailed monkey group 45–55. All groups were maintained with minimal disturbance in outdoor compounds (rhesus and pigtailed macaques: 38 × 38 m; crested black macaque and stumptailed monkeys: 30 × 30 m), with attached indoor quarters at the Yerkes Regional Primate Research Center Field Station in Lawrenceville, Georgia. Activity patterns for macaques living under these conditions have been described by Bernstein (1969, 1970, 1972). Reproduction, mortality and, infrequently, removals or additions for research, maintenance or veterinary reasons, have determined the make-up of the Yerkes groups. Matrilineal genealogical and dominance relationships (based on the direction of dyadic agonistic encounters) were known for all individuals born into the study groups, all of which were formed at least 15 years prior to the start of data collection.

Data Collection and Scoring

We collected data from observation towers or from ground level just outside the compounds from January 1983 to December 1994. Vocalizations were recorded with Uher 4000 Report Monitor or Sony TCM-5000 tape recorders and Sennheiser directional microphones (model MKH 816) equipped with foam windscreens. At least two observers were involved in data collection: one tape-recorded screams while another recorded details of the agonistic event, including the identities of the individuals involved and behaviour that preceded and followed the call. Thus agonistic encounters could later be classified according to the dominance ranks of the opponents and the nature of the aggression. The monkeys were prevented access to the indoor quarters during recording sessions. Although we attempted to record all vocal events during agonistic encounters using an all-occurrences sampling technique (Altmann 1974), complete records were not always possible when, for example, several fights erupted simultaneously.

The acoustical comparisons for the four species included in this study are noteworthy because they are based on calls and concomitant behavioural data recorded by one set of observers with the same recording equipment, under comparable recording conditions, and from animals of each species living in similar settings.

Call Selection Procedures

For each macaque species, we chose 100 screams for acoustic analysis from our library of calls. We used several selection criteria, the first of which was that calls had to be of sufficient quality to permit analysis. Only screams produced by victims of attack that involved contact aggression from a higher-ranking, unrelated opponent were included. Following Bernstein & Ehardt's (1985) categories, contact aggression included pulling, pushing, slapping, grappling and biting. All calls selected were as close to the point of contact aggression as our scoring would permit: in almost all instances calling occurred after the contact aggression had taken place and screams chosen were from the first part of the vocal bout that ensued. The proportion of calls coming from fights that involved biting was similar for all four species (*M. mulatta* 88%, *M. arctoides* 86%, *M. nemestrina* 82%, and *M. nigra* 78%; χ^2_3=4.28, NS). All vocalizations came from post-pubertal females with the exception of one 3-year-old crested black macaque, included because the *M. nigra* group, the smallest of the four, contained only nine sexually mature females. The number of females per group whose screams were included and the range of calls contributed (in parentheses) were: *M. mulatta* 16 (6–9), *M. nemestrina* 15 (5–10), *M. arctoides* 14 (6–10) and *M. nigra* 10 (5–15). No more than five calls came from any given agonistic interaction; calls selected from the same vocal bout were chosen on the basis of having been close in time to the point of contact aggression, usually near the start of calling. Calls were not included if the victim was under attack from more than one opponent. Thus, for an interaction that was initially dyadic and became polyadic, we used only calls associated with the first part of the fight.

Vocalization Analysis

We used the Signal digital sound analysis program (Beeman 1992), run on an IBM-compatible 80486 computer, to digitize the calls and screen them for selection, and we used an Apple Macintosh computer-based sound analysis program, Signalyze (Keller 1994), for the acoustic analyses. Sampling rate was set at greater than 2.5 times signal bandwidth, which was determined by sampling at the highest possible rate and measuring the maximum frequency in the spectrogram display. For each scream, we generated waveform and spectrogram windows (full-range, narrowband spectrogram setting, 25 ms/40 kHz). We took time measurements directly from the waveforms, and made frequency measurements from the spectrograms or the spectrum windows generated from specific sections of the waveform (Table 1). Although the

Table 1. Acoustic variables measured for each scream

Acoustic variable	Description
Duration	Call length (ms)
Onset frequency	Beginning frequency (kHz) of call
Peak frequency	Highest frequency (kHz) within call
Termination frequency	Frequency (kHz) at the endpoint of call
Onset–Peak	Onset frequency minus peak frequency (kHz)
Onset–End	Onset frequency minus termination frequency (kHz)
Peak–End	Peak frequency minus termination frequency (kHz)

variables we examined here are inadequate to characterize fully the overall acoustic structure of these complex vocalizations (see Owren & Bernacki 1998), our aim was not to provide definitive acoustic profiles of these screams but instead to choose variables and an analytic approach parallel to those used in previous studies examining mammalian vocalizations in the context of MS rules (e.g. August & Anderson 1987; Hauser 1993).

To guard against multicollinearity and singularity that occur when variables are perfectly correlated, or when one score is a linear combination of others, we examined squared multiple correlations between each variable and all others and, following Tabachnick & Fidell (1983), considered any correlations in excess of 0.95 indicative of redundant variables.

Statistical Analysis

We used the Windows95 version of SPSS (6.3) discriminant analysis to determine whether the 400 vocalizations could be assigned to the correct caller species on the basis of the acoustic measures. Thus, the four species were the grouping variable and the acoustic variables were the predictor variables, which were entered simultaneously (direct discriminant function analysis model). We assessed the stability of the classification procedure through a cross-validation discriminant analysis in which 25 randomly selected calls from the 100 calls for each species were withheld from the calculation of the discriminant functions. These withheld calls were then classified using the functions thus derived. Following the recommendations of Pimentel & Frey (1978), we first examined the variables for univariate cross-context differences using analysis of variance (ANOVA) and Student–Newman–Keuls multiple range tests.

Ethical Note

As advocated by Huntingford (1984), we collected all data from naturally occurring agonistic encounters; fights were not induced or staged. All nonhuman primates at the Yerkes Center are monitored by its researchers, technical and veterinary staff for injuries and wounds of any kind, including those resulting from fights that occur among socially living animals, and appropriate treatment is administered as required.

RESULTS

Univariate Analyses of Acoustic Variables

First, we examined the acoustic variables for univariate species differences to assess the importance of each singly. Means and standard deviations for each variable as well as the univariate *F* ratios and probability levels for the acoustic variables are shown in Table 2. All the measured variables showed statistically significant species differences.

We employed Student–Newman–Keuls multiple range tests to determine which species pairs differed significantly ($P<0.05$) for each acoustic variable. Mean call duration differed for all species pairs except for the *nemestrina–arctoides* contrast. All species pairs differed with respect to onset and peak frequencies as well as onset–peak and onset–end composite variables. For termination frequency, all pairs differed significantly except for the *nemestrina–arctoides* contrast. Finally, peak–end differences were significant for all species pairs except the *nemestrina–mulatta* contrast.

Discriminant Analysis

We examined the data with respect to assumptions regarding linearity, multivariate normality and homogeneity of variance–covariance matrices. No outliers were identified, there were no missing data, and call sample size was equal for the four species. Two variables failed the tolerance test (Tabachnick & Fidell 1983) for multicollinearity and singularity (i.e. they either showed too high a correlation with another variable, or proved to be a linear combination of others): onset–end and peak–end

Table 2. Univariate statistics (mean, SD) and ANOVA for the acoustic variables measured for each species

Variable	*M. arctoides*		*M. mulatta*		*M. nigra*		*M. nemestrina*		df	F	P
Duration (SD)	998	(558)	611	(269)	219	(113)	920	(367)	3,396	94.3	<0.0001
Onset (SD)	1.45	(0.46)	2.26	(0.55)	0.64	(0.27)	3.70	(0.58)	3,396	746.37	<0.0001
Peak (SD)	4.60	(0.73)	7.22	(0.58)	6.40	(1.06)	5.79	(1.48)	3,396	116.89	<0.0001
Termination (SD)	2.23	(0.77)	3.37	(0.85)	1.01	(0.61)	2.13	(0.85)	3,396	154.90	<0.0001
Onset–Peak (SD)	−3.12	(0.84)	−4.96	(0.86)	−5.77	(1.10)	−2.10	(1.49)	3,396	226.09	<0.0001
Onset–End (SD)	−0.81	(0.91)	−1.11	(0.94)	−0.37	(0.66)	1.57	(1.06)	3,396	177.46	<0.0001
Peak–End (SD)	2.37	(1.05)	3.85	(1.07)	5.40	(1.19)	3.67	(1.77)	3,396	89.60	<0.0001

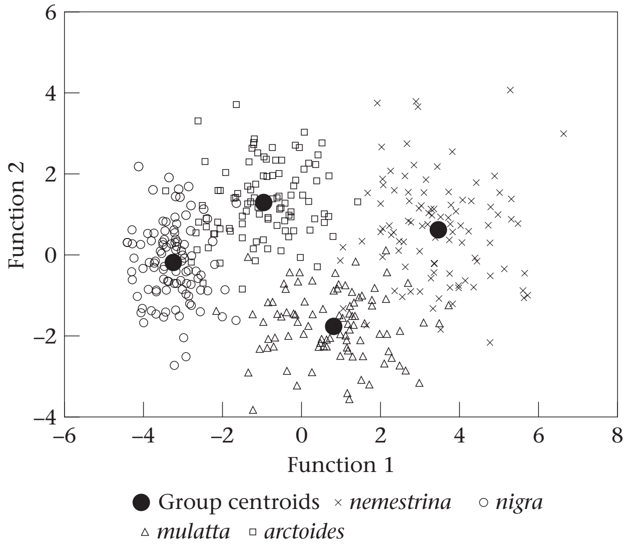

Figure 1. Species centroids and scatterplot of discriminant scores for calls on the first two discriminant functions.

frequencies. These two variables were not included in the discriminant analysis run.

We obtained three discriminant functions with a combined $\chi^2_{12}=1348.55$, $P<0.0001$. There was still significant discriminating power after removal of the first and second functions ($\chi^2_6=573.87$, $P<0.0001$ and $\chi^2_2=243.72$, $P<0.0001$, respectively). The three discriminant functions accounted for 74, 16 and 10% of the variability among species for these acoustic measures. Figure 1 shows a plot of the four species' centroids (multivariate means) on the first two discriminant functions and scatterplots for the discriminant scores. The first discriminant function maximally separated the crested black macaque from the pigtailed macaque groups, while the second discriminated the rhesus monkeys from the stumptailed macaques. The centroids for the four species showed clear separation from one another.

Classification Results

A large majority of screams were successfully classified as to the caller's species: of 400 vocalizations, 93.5% were assigned to the correct species (Table 3), a significantly better rate than predicted by chance (25%). For stumptailed macaques, 87 of the 100 screams were correctly classified, where only 23 would be expected by chance. Rhesus macaque screams were successfully assigned to the caller's species in 93 of 100 instances (25 expected) and 98 of 100 crested black macaque calls were classified correctly (27 expected). For pigtailed macaques, 96 of 100 calls were accurately assigned (25 expected). The calls of all four species were thus assigned at highly significant rates to their correct species.

The SPSS discriminant analysis program reports probabilities of group membership that are based on proximity of a call's discriminant function score to the centroids. Figures 2–5 show sound spectrograms of screams of the four species that were correctly assigned to the caller's species with a probability of greater than 0.90.

A total of 26 calls were assigned to an incorrect species. By species, 13 of these were from stumptailed macaques, seven from the rhesus, four from the pigtailed monkeys, and only two from the crested black macaques. The majority of incorrectly assigned screams were classified as crested black macaque calls (11), while each of the other species had five incorrect assignments. All 11 of the calls incorrectly classified as crested black macaque screams were produced by stumptailed macaques. Figure 6 shows sound spectrograms of seven of these incorrectly assigned screams. Assignment probabilities for these calls ranged from relatively low (0.48–0.67) for calls (b), (f) and (g) to quite high (0.80–0.88) for calls (a), (c), (d) and (e).

In the cross-validation discriminant analysis, 284 of the 300 vocalizations (94.7%) from which the discriminant functions were generated were classified correctly as to caller species, a rate not significantly different from that obtained in the analysis based on the total of 400. The rate of successful classification for the 100 calls withheld for cross-validation was 89%, which also did not differ significantly from the proportion of correctly assigned calls for the 300 used to generate the discriminant functions $\chi^2_2=2.72$, $P>0.05$, Yates' correction for continuity applied).

DISCUSSION

These analyses revealed that each of the four macaque species use acoustically distinct screams in a shared context, receiving contact aggression from a higher-ranking opponent. Our previous work on rhesus and pigtailed macaques (Gouzoules et al. 1984, 1998; Gouzoules & Gouzoules 1989), as well as the misclassifications resulting from the present analyses, suggest that each of the

Table 3. Discriminant function classification of screams according to caller species

Correct species	*N* (calls)	Predicted species membership			
		M. arctoides	*M. mulatta*	*M. nigra*	*M. nemestrina*
M. arctoides	100	87	2	11	0
M. mulatta	100	2	93	0	5
M. nigra	100	2	0	98	0
M. nemestrina	100	1	3	0	96
Percentage of calls classified correctly: 93.50%					

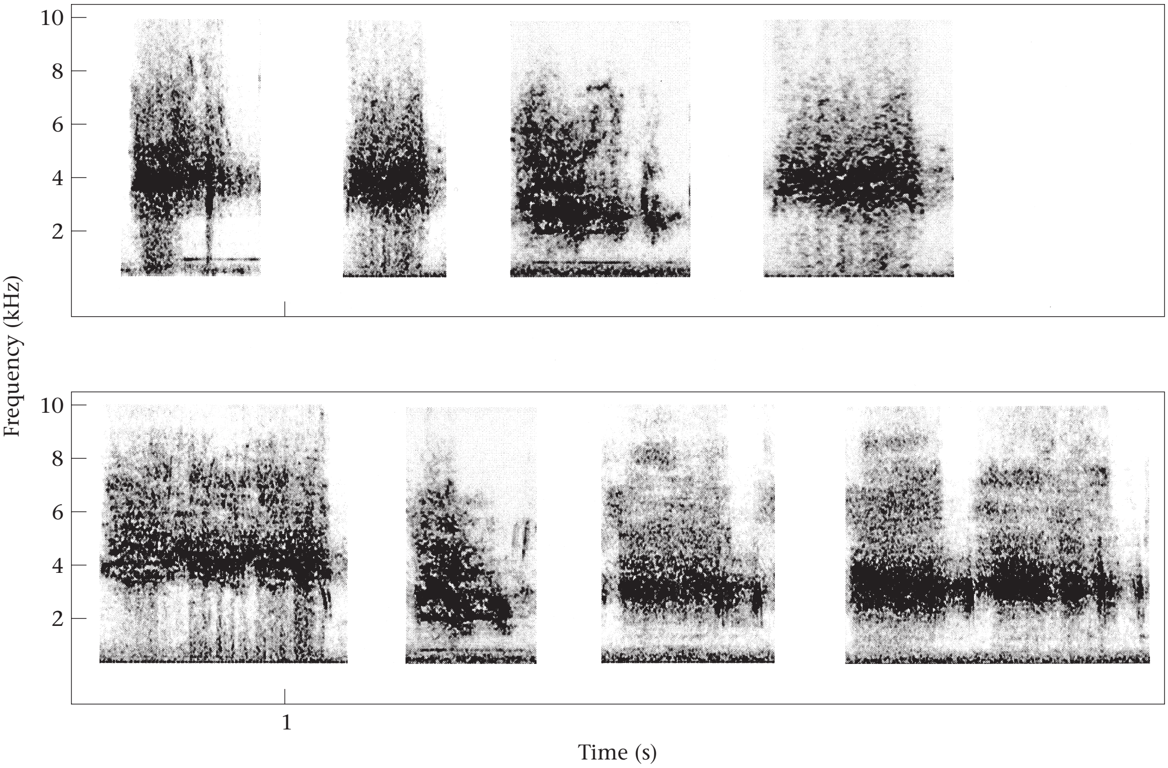

Figure 2. Sound spectrograms of some of the rhesus macaque screams that were correctly assigned to the caller's species with a probability of greater than 0.90.

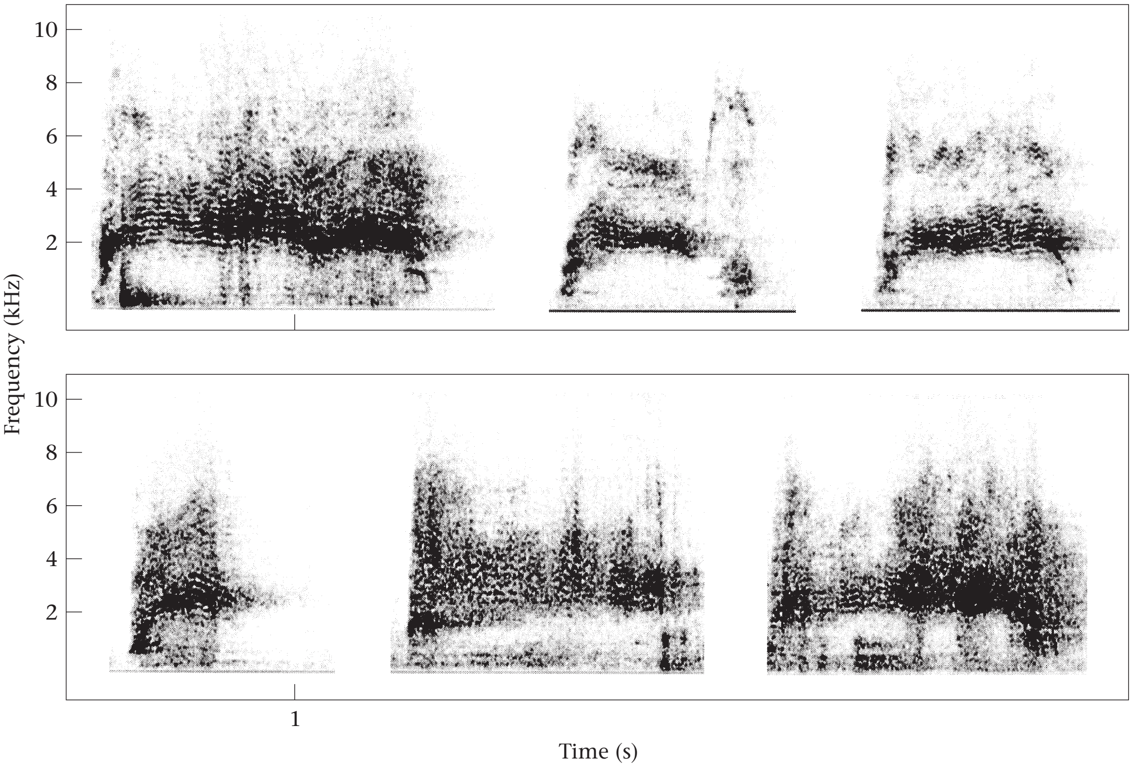

Figure 3. Sound spectrograms of some of the stumptailed macaque screams that were correctly assigned to the caller's species with a probability of greater than 0.90.

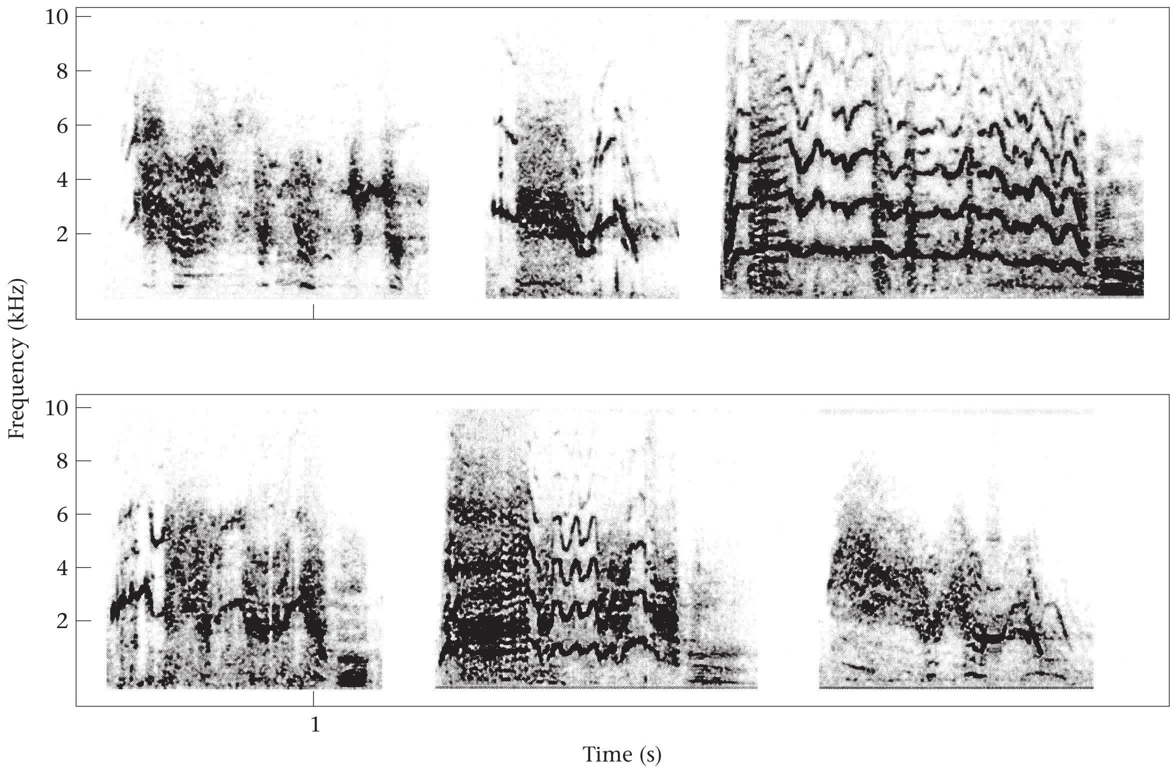

Figure 4. Sound spectrograms of some of the pigtailed macaque screams that were correctly assigned to the caller's species with a probability of greater than 0.90.

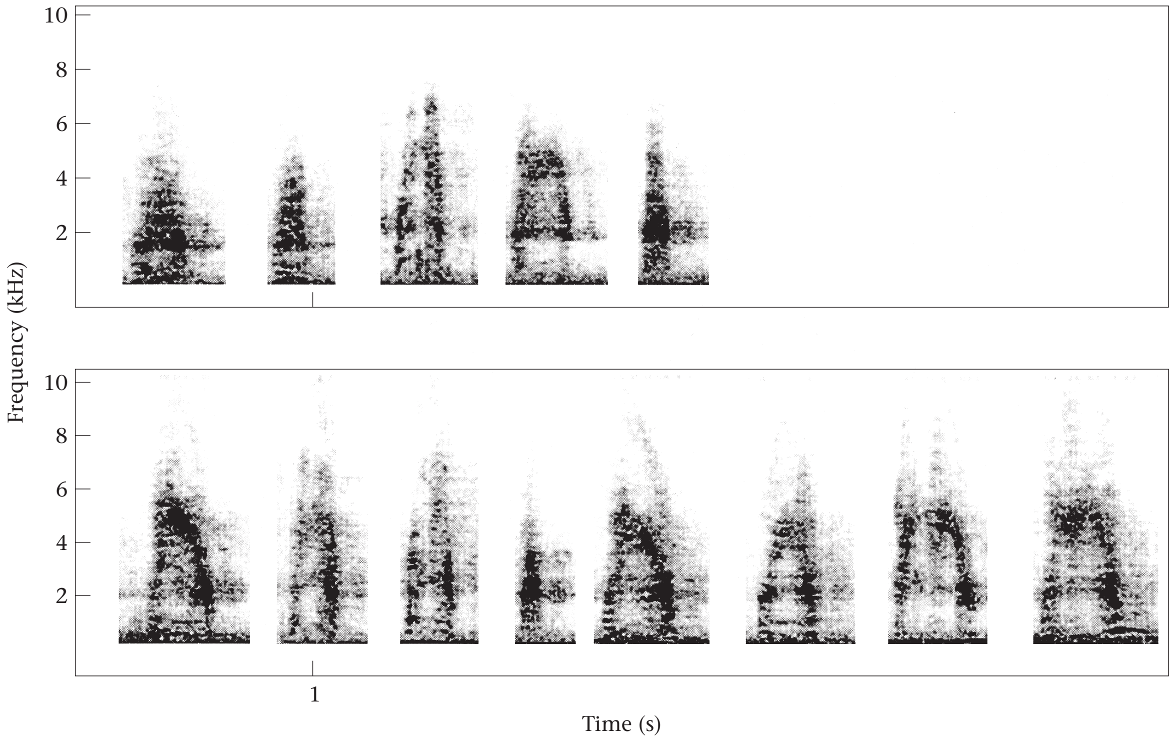

Figure 5. Sound spectrograms of some of the crested macaque screams that were correctly assigned to the caller's species with a probability of greater than 0.90.

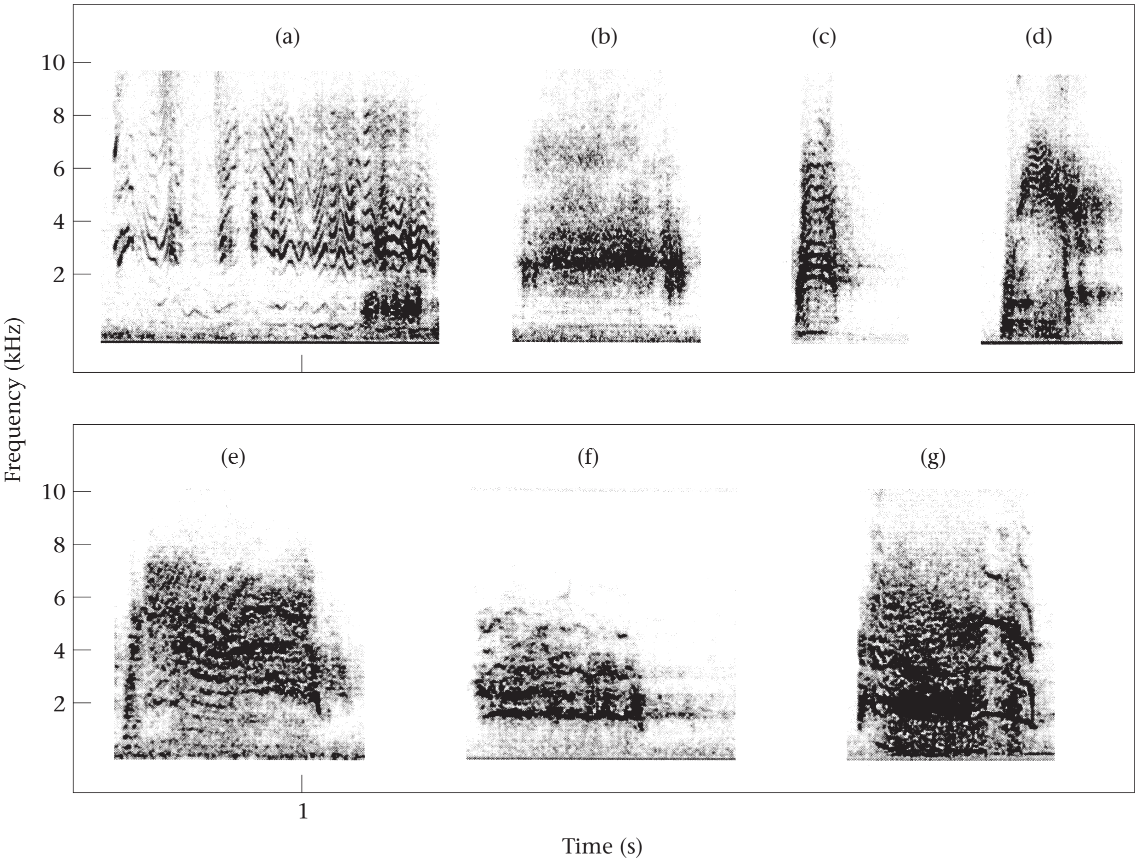

Figure 6. Sound spectrograms of several incorrectly assigned screams. (a) Rhesus macaque call classified as pigtailed macaque. (b) Rhesus macaque call classified as stumptailed macaque. (c, d) Stumptailed macaque calls classified as crested macaque. (e) Crested macaque call classified as stumptailed macaque. (f, g) Pigtailed macaque calls classified as rhesus macaque. Assignment probabilities: range 0.48–0.67 for calls (b), (f) and (g); range 0.80–0.88 for calls (a), (c), (d) and (e).

four species is physically capable of producing screams that are similar to those found in the repertoires of the other species, which is not surprising given the similarity among members of the genus in the mechanisms underlying phonation (Hauser 1996a, page 479).

That the four macaque species we examined use distinctly different screams is a finding at odds with Owings & Morton's (1998, page 115) observation that screams often lack species-typical attributes. Their argument was based on the fact that screams in many species are produced in response to attacks from predators that are usually of a different species. It might be adaptive for such calls to be of a similar acoustic structure either because they serve to startle the predator, attract others (conspecifics or not) to mob the predator, or lure an even larger predator, which might chase the first one away. A significant difference, then, for macaque screams is that they are most prominent and common during intraspecific aggression, and suggestions for understanding their acoustic structure must relate to the nature of this largely within-group conflict. Although fear and pain are likely consequences for the victims of severe aggression in each macaque species, there appears to be no simple correspondence between the acoustic structure of the four macaques' screams and the predictions from Morton's MS rules. Pigtailed macaque screams given in this context have a largely tonal form with harmonics present and, on average, have a higher onset frequency (mean 3.70 kHz) than termination frequency (mean 2.18 kHz). Rhesus and stumptailed macaques' screams are mostly atonal and broadband in nature (although those of the stumptailed macaques have a more nasalized sound, perhaps due to the presence of very narrow energy bands, and there is a tendency for the frequency to rise sharply at the call's beginning and to decrease towards the end). Calls of the crested black macaques are of the shortest duration and take the 'chevron' form that, according to the MS rules hypothesis, is indicative of an intermediate state between fear and aggression. One level of explanation for these differences comes from Owings & Morton's (1998, page 127) contention that MS rules are less likely to be in effect for long-distance vocalizations. If screams, which are the loudest calls in the macaque vocal repertoire, function to solicit support from spatially distant allies, their structure might be expected to deviate from that predicted by the MS rules hypothesis. This possible emancipation from MS rules does not, however, explain why the four species make use of acoustically different screams, nor does it account for the specific form of each species' calls.

Recently, Owren & Rendall (1997) proposed an affect-conditioning model of nonhuman primate vocal communication in which they argued that a Pavlovian conditioning framework can account for important aspects of how calls function to influence the behaviour of conspecific receivers. They, with Owings & Morton (1998), have tried to move away from the 'informational' perspective, common in communication studies (reviewed in: Hauser 1996a; Bradbury & Vehrencamp 1998), that signals make available information to which a receiver may respond. Owren & Rendall's model attempts to account for the basic design and function of primate vocalizations by viewing the sounds as stimuli that senders use to elicit simple affective responses in receivers. They envisage roles for both unconditioned and conditioned responses in the manner by which behaviours are elicited by vocalizations but, with respect to screams, the former type of learning is suggested to be strongest. They reason that, due to general properties of the mammalian auditory system, a call can elicit negative or positive reactions; negative reactions are thought to be associated with high amplitude and overall noisiness in calls. They suggest primate screams as an example of calls that produce unconditioned, negative responses in receivers, something they argue would discourage impending or ongoing aggression from a higher-ranking attacker. A subordinate monkey's most effective vocal solution to the problem of attack from a higher-ranking opponent would therefore be to use sheer magnitude and raw features of acoustic signals for inducing aversive unconditioned responses in opponents (Owren & Rendall 1997, page 330).

Although there are other perspectives on the options available for the subordinate attack victim and the function of screams, for example, vocal recruitment of support (reviewed in Gouzoules et al. 1995), the issue most relevant to the macaque vocal data presented here is that of scream structure. While all four macaque species' screams are loud, the variation in call structure among species does not appear to be explained by the affect-conditioning model. Based on the starting assumption that general properties of the mammalian auditory system predispose the monkeys to react negatively to certain call properties, it is not clear why closely related species should have evolved such acoustically distinct screams if they serve as unconditioned stimuli that are naturally repugnant to aggressors.

A key to understanding these vocal differences might come from a broader view of the nature of aggression and the reactions to it in these species. While all four species have similar social organizations and monkeys of each experience contact aggression from higher-ranking opponents, there are notable differences. Bernstein et al. (1983) compared agonistic behaviour of the four species of macaques at the Yerkes Center. Their data were collected from the same groups included in our study and are thus of particular interest. Other studies have compared agonistic behaviour and reconciliation in some of the species we studied and provide additional comparative perspectives (Thierry 1985, 1986; de Waal & Ren 1988; Petit et al. 1997). Bernstein et al.'s (1983) study found that rhesus and stumptailed macaques had the highest hourly rates of agonistic expression. The crested and the pigtailed macaques had hourly rates that were less than half that of the rhesus monkeys. Stumptailed macaques had the highest rate of contact aggression, followed by the rhesus, the crested macaques and the pigtailed monkeys. Biting had the highest rate of occurrence in the rhesus, followed by stumptailed monkeys, the crested macaques and the pigtailed monkeys. While the hourly rate of third-party participation in aggression was highest in the rhesus monkeys, there was a larger percentage of aggressive encounters involving more than two animals in pigtailed macaques than in those of the other species examined. In general, relatively little agonistic aiding was seen in the crested macaques, though immature females of this species were aided often (Bernstein et al. 1983, page 121). Contact aggression among the crested macaques consisted largely of manual forms, and biting by adult males was rare. Petit et al. (1997) also found that aggressive manual contacts were high in their crested macaque study, but that peaceful interventions were common (Petit & Thierry 1994; Petit et al. 1997). Reconciliation rates have been reported to differ among these macaques (stumptailed macaques: 56% of fights, de Waal & Ren 1988; crested macaques: 41%, Petit & Thierry 1994; pigtailed macaques: 40%, Judge 1991; and rhesus macaques: 20%, de Waal & Ren 1988). Wounding data covering a 21-month period for the Yerkes macaque groups (Ruehlmann et al. 1988) revealed that 49.4% of adult and juvenile female rhesus macaques received visible fight wounds, while for pigtailed macaques the proportion was 54.5% and, for stumptailed macaques, 60%. The crested macaques did not show wounding frequently enough to be included in their analysis, a finding mirrored in Petit et al.'s (1997) study.

On the basis of the above comparisons, the four macaque species can be ranked loosely in terms of the severity of aggressive interactions (Table 4). Rhesus macaques appear to have the most severe forms of aggression, followed by stumptailed and pigtailed macaques, with the crested macaques exhibiting the least serious patterns. Primate dominance patterns have been described as either 'despotic' or 'egalitarian' on similar grounds, and macaque species seem to fall along a grade between these endpoints (de Waal 1989; Thierry 1990; Butovskaya 1993). Rhesus tend to be classified towards the despotic end, whereas stumptailed, pigtailed and especially crested macaques appear more egalitarian.

While the differences in the macaque species' vocalizations described here suggest no simple correlation between immediate context (biting from a higher-ranked opponent and the pain and fear presumably experienced) and the acoustic forms of screams, there appears to be some correspondence between the acoustic structure predicted by MS rules and inferences about the internal state of the vocalizer derived from the 'general' patterns of aggression in each of the four species (Fig. 7). For example, the chevron-shaped vocalization of the crested macaque falls between the fear and aggression endpoints; the aggressive patterns in this species, and the consequences for the victim of being attacked, seem to be the least severe. The calls of pigtailed, stumptailed and rhesus

Table 4. Agonistic behaviour ratings of the four macaque species

	M. mulatta	*M. nemestrina*	*M. arctoides*	*M. nigra*
Hourly agonistic rate*	1	4	2	3
Hourly aggression rate*	2	3	1	4
Contact aggression rate*	2	4	1	3
Biting*	1	3.5	2	3.5
Wounding†	3	2	1	4
Reconciliation rates‡	1	2	4	3
Mean rank	1.67	3.08	1.83	3.42

Reconciliation rates are ranked from lowest (1) to highest (4).
*Bernstein et al. 1983.
†Ruehlmann et al. 1988.
‡de Waal & Ren 1988; Petit & Thierry 1994; Judge 1991.

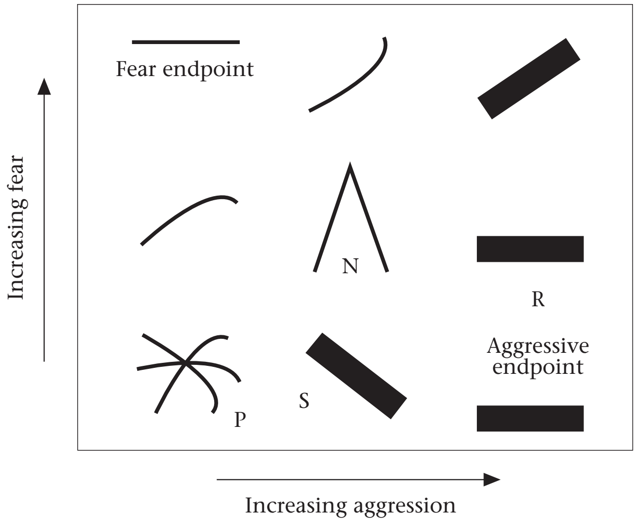

Figure 7. Diagrammatic representation of vocal forms in the motivation-structural code and the approximate placement of the scream types of the four macaque species within the MS scheme. Narrow lines represent tonal sounds, thicker lines represent harsh or broadband sounds. Vocal forms grade from high-pitched and tonal (fear endpoint) to low-pitched and harsh (aggressive endpoint). Motivation weakly tends towards aggression if the narrow or thick lines slope downward and towards fear if they slope upward. The central chevron shape in the middle is the vocal form squarely between the fear and aggressive endpoints. Species designations are: R: rhesus macaque; S: stumptailed macaque; P: pigtailed macaque; N: crested macaque (redrawn from Owings & Morton 1998, page 114).

macaques are arranged along the increasing aggression axis in line with the degree of severity of each species' aggressive patterns. While screams of pigtailed macaques are more tonal than those of stumptailed macaques, and thus fall further from the aggressive endpoint, calls of both species tend to drop in pitch towards the aggressive endpoint. Screams of rhesus macaque appear closest to the aggressive endpoint and neither rise nor fall in pitch; their aggressive interactions are more severe than those of the other species.

While only the most intense context for aggression recorded (contact aggression from a higher-ranking opponent) was considered in this study, other contexts were noted for each species. Noncontact aggression (e.g. stares and vocal threats) was common and attacks from lower-ranking opponents also took place. In pigtailed and rhesus macaques, calls associated with some of these other agonistic contexts have been described (Gouzoules et al. 1984; Gouzoules & Gouzoules 1989). Rhesus macaques, for example, attacked by lower-ranking opponents often make use of 'arched screams' that rise and fall sharply in pitch (see Figure 1 in Gouzoules et al. 1998). The arched scream thus bears some structural resemblance to the call used by crested macaques confronted by contact aggression from higher-ranking opponents. A scream type used by pigtailed macaques confronted by lower-ranking opponents also takes this same basic form. One speculation suggested by these similarities is that, with their more egalitarian dominance systems, the average internal state of crested macaques facing a higher-ranking opponent and the most severe form of aggression shown by the species, might be more similar to that experienced by the more despotic rhesus monkey and the pigtailed monkey, with its intermediate dominance style, when they encounter minimally serious aggression from lower-ranking group members. We emphasize average internal state in this comparison because, from an evolutionary perspective, the typical intensity of the emotional/motivational state of ancestral individuals probably dictates the acoustic structure of the vocalization selected for use in a particular context. This argument is supported by considerable evidence indicating that monkey vocal production is largely under genetic control (Snowdon & Elowson 1992; Seyfarth & Cheney 1997).

Owings & Morton (1998, page 116) have contended that because a specific acoustic structure has a particular motivational significance and function, the range of situations in which that structure will occur is limited. Their argument, again, is primarily for short-range vocalizations and might not apply completely to screams that are involved in recruitment of distant allies. It seems reasonable to imagine, though, that primate screams and their acoustic structures pre-date, evolutionarily, current uses in agonistic recruitment: screams are more widely documented across different species than is agonistic aiding (Gautier & Gautier 1977; Walters & Seyfarth 1987;

Hauser 1996b). Any selection that has operated to make these calls effective in agonistic recruitment in some species has likely centred on receivers. A narrow interpretation of what constitutes 'situation' would render our results at odds with Owings & Morton's claim, but by broadening the sense to encompass the typical intensity of aggression for each macaque species, there is greater compatibility. Our results suggest that within an identically defined situation across closely related species, more general features of a social system, such as the dominance styles and aggressive patterns of macaques, might have ultimate effects on the acoustic structure of calls used and, perhaps, the internal state of the caller.

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