

# Motivation before Meaning: Motivational Information Encoded in Meerkat Alarm Calls Develops Earlier than Referential Information

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**ABSTRACT:** In contrast to historical assumptions about the affective nature of animal vocalizations, it is now clear that many vertebrates are capable of producing specific alarm calls in response to different predators, calls that provide information that goes beyond the motivational state of a caller. However, although these calls function referentially, it does not mean that they are devoid of motivational content. Studies on meerkats (*Suricata suricatta*) directly support this conclusion. The acoustic structure of their alarm calls simultaneously encodes information that is both motivational (level of urgency) and referential (predator specific). In this study, we investigated whether alarm calls of young meerkats undergo developmental modification and whether the motivational or the referential aspect of calls changes more over time. We found that, based on their acoustic structure, calls of young showed a high correct assignment to low- and high-urgency contexts but, in contrast to adults, low assignment to specific predator types. However, the discrimination among predator types was better in high-urgency than in low-urgency contexts. Our results suggest that acoustic features related to level of urgency are expressed earlier than those related to predator-specific information and may support the idea that referential calls evolve from motivational signals.

**Keywords:** meerkats, alarm calls, development, referentiality, motivational signals.

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Animal signals have historically been thought to lack the capacity to function referentially, that is, providing listen-

ers with information about external objects or events, one of the key characteristics of human speech. Instead, vocalizations of animals have been seen as mainly reflecting the caller's motivational state (reviewed in Marler et al. 1992; Seyfarth and Cheney 2003). Studies over the past 20 years have created a more complicated picture, acknowledging the fact that animal signals, like human speech, can encode specific information linked to external stimuli that goes beyond the motivational state of a signaler (see Seyfarth and Cheney 2003). Nevertheless, no animal or human signal that has been identified as referential is devoid of motivational content, although the proportional contributions of each component may vary widely within and between species (e.g., Marler 1977; Marler et al. 1992; Macedonia and Evans 1993; Bachorowski and Owren 1995; Seyfarth and Cheney 2003). The same vocalization therefore has the potential to convey information both about an external referent and about the caller's level of emotion. Recent research has also led to a general agreement that "motivation" and "reference" are logically distinct and independent dimensions. Even if animal signals are pure expressions of the callers' emotions, as long as they are elicited by specific stimuli, they can convey referential information to listeners (reviewed in Seyfarth and Cheney 2003).

Alarm calls are particularly well suited to address questions regarding the relative role of referentiality and motivation in animal signals (Macedonia and Evans 1993; Evans 1997; Blumstein 2002). Many species of nonhuman primates (reviewed in Macedonia and Evans 1993; Zuberbühler 2000, 2001) and also chickens (*Gallus gallus domesticus*; Evans et al. 1993) give acoustically distinct alarm calls in response to different types of predators, whereas alarm calls of other species, such as ground squirrels (*Spermophilus* sp.) and marmots (*Marmota* sp.), lack the high degree of referential specificity and reflect differences in response urgency perceived by the caller (reviewed in Macedonia and Evans 1993). However, it is likely that, together with contextual cues, the alarm calls of ground-

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dwelling sciurids may provide listeners with probabilistic identification of predator types. Similarly, the production specificity of nonhuman primate alarm calls varies, suggesting that variation in motivational state of a caller plays an important role in the production of the specific calls (Macedonia and Evans 1993). Thus, it seems likely that vocal signals in a wide array of species have both referential and motivational characteristics, as has been shown in human speech (e.g., Bachorowski and Owren 1995). Recent work on the alarm calls of meerkats (*Suricata suricatta*) directly supports this conclusion and clearly demonstrates the entwined role of motivation and reference in animal communication (Manser 2001; Manser et al. 2002).

While animal vocalizations can be both motivational and referential in the information they convey, we know little about how the characteristics encoding such information develop. Children seem to enter the language system of word use through the use of vocal forms that are more adultlike in sound than in their semantic function and may stimulate participation in social interactions rather than transmitting information (Locke and Snow 1997). To our knowledge, no study on nonhuman vocal production has investigated whether, like in children, referential aspects of calls develop later than other aspects. Since we know the role of motivation and reference in meerkat alarm calls and the acoustic features encoding this information, meerkats provide a good opportunity to investigate how these two different attributes of calls develop.

Meerkats are small, cooperatively breeding mongooses inhabiting the arid regions of southern Africa (Clutton-Brock et al. 1999b). They are preyed on by several raptors, mammalian predators, and snakes (Clutton-Brock et al. 1999a), which elicit acoustically distinct alarm calls (Manser 2001). Additionally, within each call class, the acoustic structure of calls varies depending on the distance to the predator. Calls given in response to predators close by (termed "high urgency") are acoustically different from those given in response to the same predator encountered at a far distance (termed "low urgency"). Listeners thus acquire information about specific predators and the level of danger they represent, allowing them to respond appropriately in specific contexts (Manser et al. 2001). The acoustic parameters accounting for variation among predator types are different from those explaining the variation across the levels of urgency (Manser 2001). Moreover, while changes in acoustic structure along the dimension of urgency are consistent across different predator types, with calls becoming harsher and noisier as urgency increases, the referential information about each predator type is not encoded in any consistent way. The features of meerkat alarm calls might therefore support the idea that referential alarm calls evolve from motivational calls

in the repertoire (Macedonia 1993). Supporting this, we previously found that although young less than 6 months of age rarely uttered alarm calls, calls that seem to reflect intense fear were present already on the first day of emergence, whereas calls specific to particular predator types appeared much later in the repertoire (L. I. Hollén and M. B. Manser, unpublished data).

In this study, we investigated whether the acoustic aspects of calls related to referential information also undergo more developmental modification than motivational aspects. Specifically, we asked whether (i) the calls of young, as those of adults, can be classified correctly according to the context in which they are given on the basis of their acoustic structure; (ii) the discrimination along the level of urgency differs from the discrimination along predator types; (iii) the change in acoustic structure along the dimension of level of urgency is consistent across predator types; and (iv) the acoustic parameters explaining differences between adult calls can be used to correctly assign the calls of young and vice versa. Finally, we examined which acoustic parameters are important in determining variance among individuals of different ages.

## Methods

### *Study Site and Animals*

We studied the ontogeny of alarm call production in 13 groups of free-ranging but habituated (close observation <1 m) meerkats near VanZyl's Rus in the South African part of the Kalahari Desert (26°58'S, 21°49'E; details of study site provided in Clutton-Brock et al. 1999a) from January to July 2003 and from October 2003 to June 2004. All animals were marked for individual identification with hair dye or hair cuts applied to their fur noninvasively during sunning at the morning sleeping burrow. All individuals had been monitored since birth, and their exact ages were therefore known.

### *Recording Methods and Call Selection*

We analyzed calls obtained from recordings during natural predator encounters and from a manipulation experiment (see below). Alarm calls obtained during natural encounters were recorded from pups (<3 months old), juveniles (3–6 months old), subadults (6–12 months old), and adults (>12 months old). Pups from 12 litters were followed regularly (on average once per week) from their emergence (mean  $\pm$  SD: 17  $\pm$  2.4 days) until reaching subadult age. Calls from other pups, juveniles, subadults, and adults were recorded ad lib. whenever we visited a group. We also conducted a manipulation experiment in order to test the development of recruitment alarm calls

under controlled conditions. Recruitment calls are emitted in response to snakes and deposits such as fecal, urine, or hair samples of other meerkats or predators, and they are collectively termed recruitment calls since they function to recruit other group members to investigate or mob the threat (Manser 2001). We presented the meerkats with hair samples of an African wildcat (*Felis lybica*), which has been shown to reliably elicit recruitment alarm calls in adults (Graw 2005). The hair, cut from a salt-treated skin (obtained from a roadkill carcass stored in a freezer) before the experiment, was placed in front of a foraging individual. Young (<6 months) were exposed to the hair at four different stages during development (age in days [mean  $\pm$  SD]: stage 1, 41  $\pm$  6; stage 2, 78  $\pm$  7; stage 3, 114  $\pm$  6; stage 4, 161  $\pm$  17), and after each presentation, adult individuals were also tested. We tested a total of 69 young individuals (37 females and 32 males) and 43 adult individuals (18 females and 27 males) in 12 groups.

Alarm calls were recorded at a distance of 1–2 m from the caller at 44.1-kHz sampling frequency, using a Sennheiser directional microphone (ME66/K6 with an MZW66 pro windscreen; frequency response: 40–20,000 Hz  $\pm$  2.5 dB; Sennheiser, Old Lyme, CT) connected to a Sony DAT-TCO D100 digital audio tape recorder (frequency response: 20–20,000 Hz  $\pm$  1 dB, Sony, Tokyo) or a Marantz PMD-670 solid state recorder (D&M Holdings, Kanagawa). Type and distance to stimuli (naturally occurring) eliciting the calls were spoken onto the tape. Calls were uploaded to a PC (sampling frequency: 44.1 kHz; resolution: 16 bit) and visually inspected using Cool Edit 2000 (Syntrillium, Phoenix). Only those calls with sufficiently high quality were chosen for analysis.

We examined five predator-specific call types: aerial, terrestrial, and recruitment calls at low-urgency level and aerial and recruitment calls at high-urgency level (for spectrograms, see fig. 1). Terrestrial high-urgency calls were excluded because of low sample size for young individuals. In brief, aerial and terrestrial calls are given in response to aerial and mammalian stimuli, causing meerkats to scan their surroundings or move to a bolthole (Manser 2001; Manser et al. 2001). Predators at a far distance (aerial: >200 m; terrestrial: >50 m) typically elicit low-urgency calls, whereas predators close by (aerial: <200 m; terrestrial: <50 m) elicit high-urgency calls. Recruitment high-urgency calls are emitted in response to both snakes and deposits, whereas recruitment low-urgency calls are mainly given when encountering deposits (Manser 2001). We also included one call type, the growl call, that is not specifically related to a single predator type. These calls are often heard from young when nondangerous stimuli such as birds make sudden movements within a few meters of the caller. Because these calls sound similar to other predator-specific

high-urgency calls, we included them to see whether they are similar on the basis of their acoustic structure.

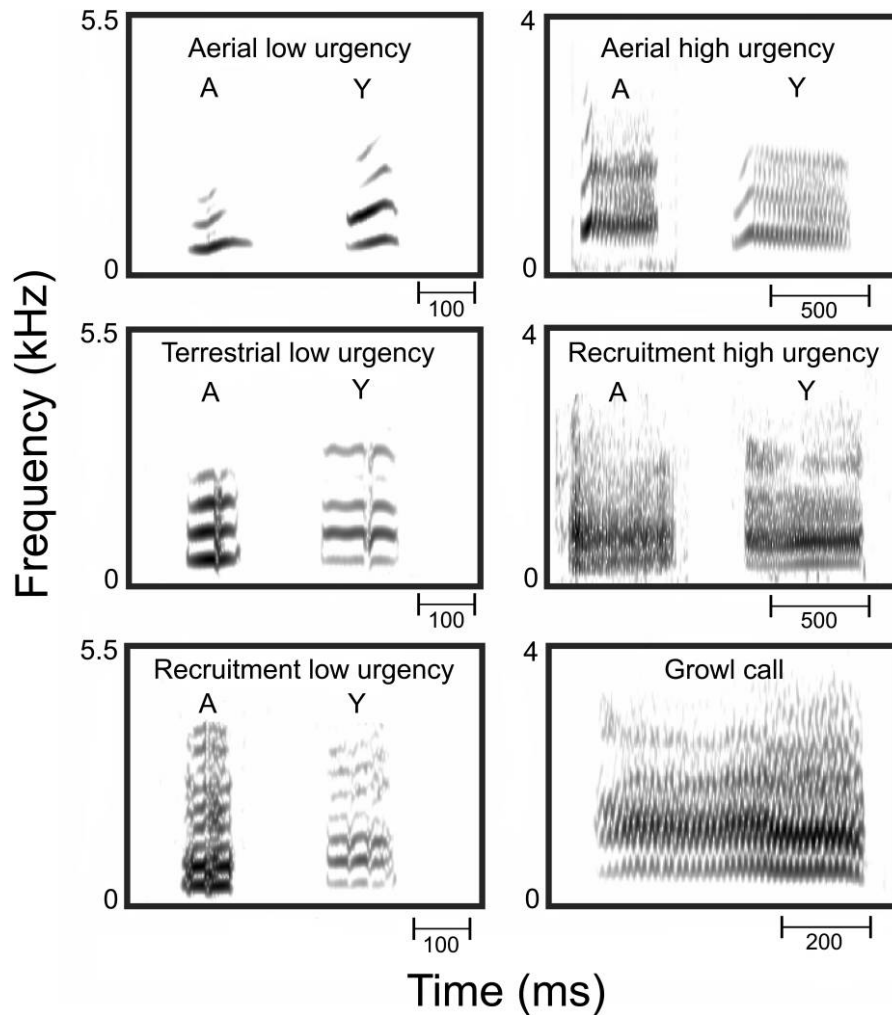
#### *Acoustic Analysis*

We first conducted a 1,024-point fast Fourier transformation (Hamming window; time step: 1.45 ms; overlap: 98.43%; frequency range: 11.025 kHz; frequency resolution: 28 Hz) of all calls using AVISOFT-SASLab pro 4.38 (R. Specht, Berlin). The resulting frequency-time spectra were analyzed with LMA 2005 (developed by K. Hammerschmidt), a software tool that extracts a large number of call parameters from acoustic signals (for detailed description of the algorithms and calculation of parameters, see Schrader and Hammerschmidt 1997). A list of the parameters used in our analyses is given in appendix A in the online edition of the *American Naturalist*.

We first calculated a set of parameters, including start, minimum, maximum, and median frequency of the first two dominant frequency bands. The dominant frequency bands are characterized by amplitudes that exceed given thresholds in a consecutive number of cells. In tonal calls, these bands represent the fundamental frequency and its harmonics, whereas in atonal signals, the dominant frequency peaks reflect the frequencies with the highest energy. Second, we determined the statistical distribution of spectral energy measured as the first and second quartiles of the distribution of frequency amplitudes in the spectrum. Third, we calculated the local and global modulation of the first dominant frequency band. Fourth, we determined the location and the modulation of the peak frequency (the frequency with the highest amplitude in a time segment). Fifth, we measured temporal parameters such as call duration and temporal location of minimum and maximum frequencies. Finally, we also determined the mean and maximum harmonic-to-noise ratio. Including many acoustic parameters allows for a comprehensive analysis of complex patterns without any a priori assumptions about the importance of specific parameters (see Schrader and Hammerschmidt 1997) and can also improve the rate of correct assignment (Hammerschmidt and Todt 1995).

#### *Statistical Analyses*

We conducted all analyses in R for Microsoft Windows, version 2.2.1 (R Development Core Team 2005), using the software packages “MASS” (Venables and Ripley 2002), “Hmisc” (Harrell 2006), “Design” (Harrell 2005), and “ipred” (Peters and Hothorn 2004). Since certain parameters measured for some call types could not be reliably estimated for other call types, the number of parameters included in the analyses varies (table 1). Sample sizes for



**Figure 1:** Spectrograms of the five different predator-specific alarm calls and the one nonspecific call (growl call, uttered by pups only) included in the analyses. Calls are exemplars from adults older than 1.5 years (A) and young individuals 4 months old or less (Y).

young and adults also vary depending on call type (table 1). Assumptions of multi- and univariate normality and homogeneity of variances were fulfilled.

We used a discriminant function analysis (DFA) method (function lda in “MASS”) to determine the classification probabilities of alarm calls uttered by young (<12 months) and adults (>12 months). Discriminant function analysis identifies linear combinations of predictor variables that best characterize the differences among groups and combines the variables into one or more discriminant functions, depending on the number of groups to be classified ( $N_{\text{functions}} = N_{\text{groups}} - 1$ ). This analysis method provides a classification procedure that assigns each call to its appropriate group (correct assignment) or to another group (incorrect assignment). For external validation, we used a 10-fold cross validation technique (function er-

rorest in “ipred”). The data are randomized and partitioned into 10 folds (sets) of approximately equal size. In each of 10 turns, nine of the folds are then used for establishing the model (training data) and the remaining fold for estimating the model’s validity (test data). Different folds are used as training and test data in each turn. To calculate assignment probabilities expected by chance, we used a bootstrap approach ( $n$  repeats = 1,000). While taking into account the initial sample sizes in the actual data, random numbers were assigned to each call class. Chance probabilities are presented with the mean  $\pm$  1 SE of all repeats. Because of questions about the use of unbalanced designs in DFA, we also conducted analyses with balanced sample sizes (randomly drawn cases) to verify that our results were not biased. Since this was not the case, we report the results with the original sample sizes.

**Table 1:** Sample sizes for the different call types included in the uni- and multivariate analyses

Call type	<i>n</i>				Variance (%)
	Adults	Young	Parameters	Principal components	
Aerial low urgency	61	38	27 (16)	5 (5)	72
Terrestrial low urgency	15	9	24 (16)	5 (5)	80
Recruitment low urgency	13	12	23 (16)	5 (5)	78
Aerial high urgency	13	6	13 (13)	4 (3)	81
Recruitment high urgency	20	9	13 (13)	4 (3)	77
Growl	...	18	13 (13)	(3)	

Note: Growl call was not included in the univariate analysis. Parameters = number of acoustic parameters from which principal components were extracted (numbers included in principal component analysis preceding discriminant function analysis are in parentheses), principal components = number of principal components included in further analyses (multivariate analyses in parentheses), variance = percent of the original variance explained by the principal components in the univariate analyses (for multivariate: >70% for all).

Moreover, the DFA was set to work on the prior probabilities of each class, which were calculated from the initial sample sizes.

To avoid correlated predictor variables in the DFA, we first conducted principal component analyses (PCAs; function `princomp` in “MASS”), which create a new set of uncorrelated variables, each of which is a linear combination of the original variables. Since the PCA needs a complete correlation matrix, we first replaced missing values among our acoustic parameters using a multiple-imputation ( $n = 20$ ) approach (function `aregImpute` in “Hmisc”; Little 2004). Components (unrotated) with eigenvalues >1 were retained (>70% of the original variance explained) and used as classifiers in the DFA. To test whether the components explaining differences between adult calls can be used to assign the calls of young and vice versa, we first conducted separate PCAs on adults and young. The components extracted from adults calls were then used as training data for the calls of young and vice versa. Finally, to test whether the change in acoustic structure along the dimension of level of urgency is consistent across predator types, we took those components explaining the difference between the high and low levels of urgency for aerial calls and investigated whether these components could also explain the high and low levels of urgency for recruitment calls. We then did the reverse and investigated whether the components for recruitment calls could explain the high and low levels of urgency for aerial calls.

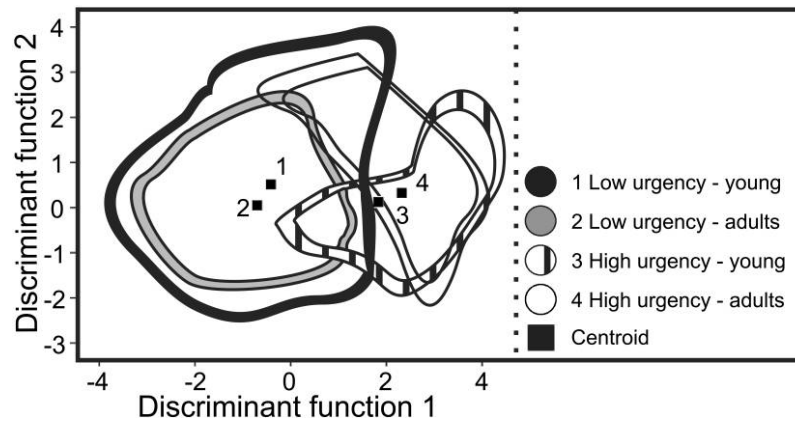
To test for univariate differences in acoustic structure of calls between individuals of different ages, we conducted a set of general linear models (function `lm` in “MASS”). For each call type, we first conducted a PCA and then used the unrotated principal components as response variables in the models (loadings of acoustic parameters on each component are provided in app. B in the online edition of the *American Naturalist*). The number of components and the amount of variation explained by these

components are displayed in table 1. Since we were sometimes not able to determine the identity of the calling individual, we pooled individuals <12 months (young) and those >12 months (adults) and fitted age as a categorical term for all call types except aerial low-urgency calls, for which we were able to fit age as a continuous (linear and quadratic) term. For aerial low-urgency calls, we also fitted, before age, factors (true or false) coding for whether individuals were younger than 3 months, younger than 6 months, or younger than 12 months. In this way, we could examine in more detail where changes during development may occur. Sex was included as an explanatory term in all models. All tests were two tailed, and the significance level was set at  $P < .05$ . Terms with  $P$  values above 0.10 were removed from the models.

## Results

### *Level of Urgency Discrimination*

For both adults and young, calls could statistically be accurately distinguished on the basis of urgency level. Adult calls (aerial and recruitment calls pooled) showed a 96% correct assignment into high- and low-urgency contexts before cross validation and 93% afterward (fig. 2). Similarly, the calls of young showed a high 92% correct assignment before and after cross validation (fig. 2). For both adults and young, this is much higher than the mean of  $52\% \pm 3\%$  expected by chance. Moreover, young tested on the calls of adults and vice versa yielded high correct assignments of 81% and 90%, respectively. When we analyzed aerial and recruitment calls separately, we also obtained high correct assignment probabilities (>85% for both young and adults). The analyses conducted to test whether the change in acoustic structure along the dimension of level of urgency is consistent across predator types yielded a mean correct assignment of  $87\% \pm 0.8\%$  for young and  $80.1\% \pm 1.4\%$  for adults, which is higher



**Figure 2:** Discrimination between calls uttered in low- and high-urgency contexts for adults and young. The outer lines represent contour lines around all data points classified to each call type.

than that expected by chance ( $50\% \pm 7\%$ ). Assignment probabilities equal to or greater than those obtained in all analyses were generated by chance in  $<3\%$  (adults =  $0.8\%$ , young =  $2.4\%$ ) of all bootstrap repeats ( $n = 1,000$ ).

#### *Predator Type Discrimination*

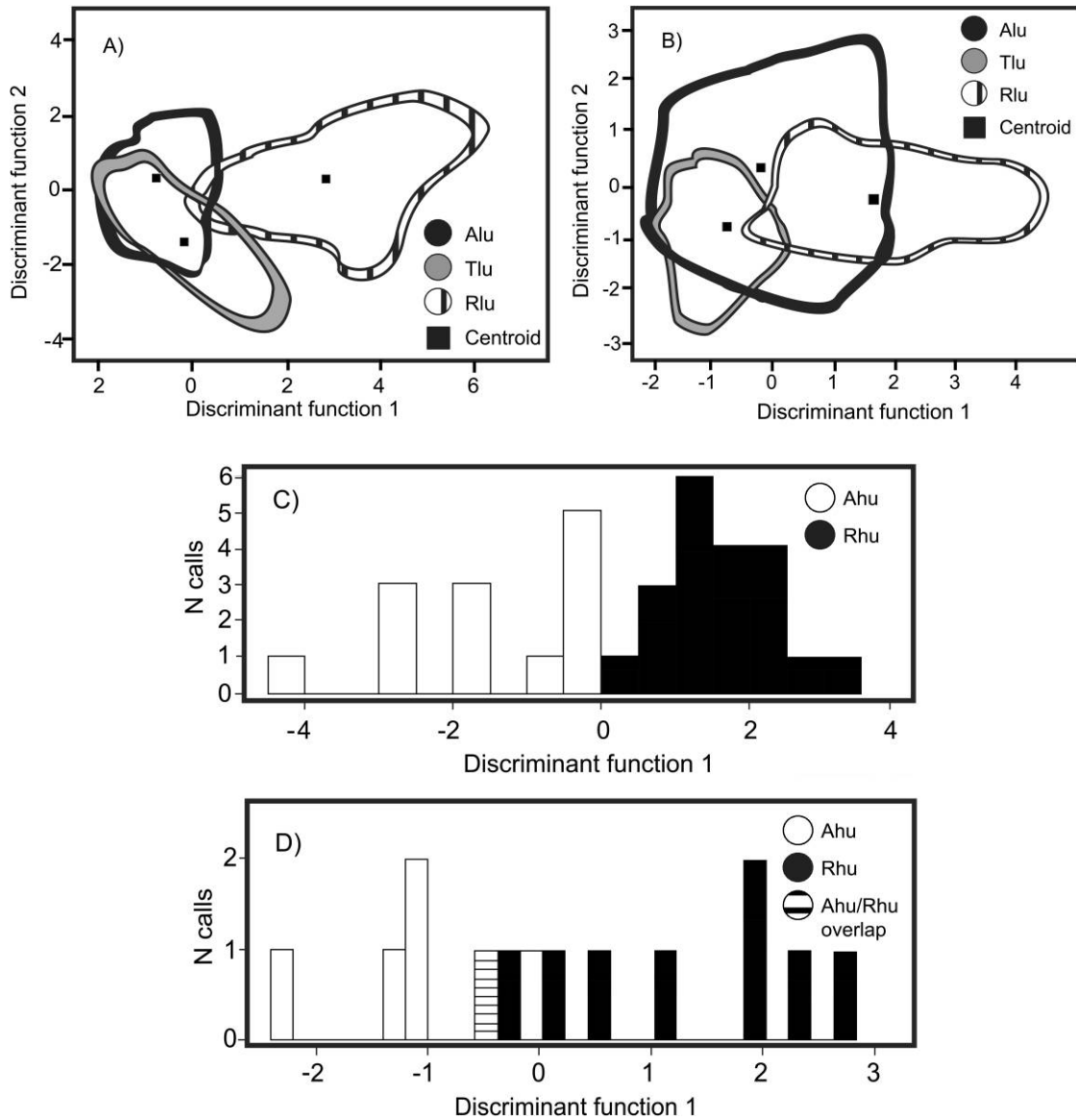
Although the calls of adults were well distinguished between predator types, calls of young showed more overlap. For calls emitted in low-urgency contexts, the DFA yielded two discriminant functions, with the first function accounting for 79% of the variance in adult calls and 86% in young. The calls of adults showed a correct assignment of 86% before and after cross validation, compared with  $42\% \pm 2\%$  expected by chance (fig. 3A; for parameters distinguishing between call types in adults, see Manser 2001). The calls of young yielded a correct assignment of 85%, but this decreased to only 63% after cross validation ( $41\% \pm 3\%$  expected by chance; fig. 3B). Although greater than that expected by chance, values  $\geq 63\%$  were obtained in 16% of all bootstrap repeats. In contrast, only 3% of the repeats for adults calls yielded values  $\geq 86\%$  by chance. Moreover, when the calls of young were tested with the principal components extracted from adult calls, they showed a correct assignment of only 46%, thus similar to that expected by chance. Similarly, if the calls of adults were tested on the calls of young, adult call assignment was reduced to 55%.

For both adults and young, the discrimination of predator types was better in high-urgency contexts than in low-urgency contexts. For calls emitted in high-urgency contexts, the DFA on adult calls yielded before and after cross validation high correct assignments of 97% and 94%, re-

spectively (fig. 3C). The calls of young showed a correct assignment of 80% before and 73% after validation (fig. 3D). For both adults and young, this is higher than the mean of  $50\% \pm 5\%$  expected by chance. Values  $\geq 73\%$  were, however, obtained in 21% of all bootstrap repeats (3% of the cases for adults yielded values  $\geq 94\%$ ). Still, when used as a test set on the adult training set, the calls of young were classified with a high correct assignment of 80%. For adults, the correct assignment stayed the same (94%) when tested on the calls of young. The second analysis including the nonspecific growl call yielded a correct assignment of 73% before and 70% after cross validation, compared with  $38\% \pm 3\%$  expected by chance. This showed that growl calls clustered relatively separately from the other high-urgency call types.

#### *Age Differences in Call Structure*

When we tested the univariate differences for those acoustic parameters reliably estimated for each call type in low-urgency contexts, aerial, terrestrial, and recruitment calls all showed some modification with age (table 2). For all three call types, there was a difference in the scores of the first principal component between individuals of different ages (aerial:  $F = 6.63$ ,  $df = 1, 92$ ,  $P = .01$ ; terrestrial:  $F = 4.46$ ,  $df = 1, 22$ ,  $P = .046$ ; recruitment:  $F = 9.09$ ,  $df = 1, 18$ ,  $P = .007$ ). For aerial and recruitment calls, the acoustic parameters highly associated with this component were parameters describing the peak frequency and the first and second dominant frequency band, with higher values in young than adults. However, for aerial calls, a significant interaction between individuals younger than 3 months and the remaining ages showed that some of the pups already had low values ( $F = 9.98$ ,  $df = 1, 92$ ,



**Figure 3:** Classification results from the discriminant function analyses on predator-specific alarm calls emitted in low-urgency (A, B) and high-urgency (C, D) contexts by adults (A, C) and young (B, D). *Alu* = aerial low urgency, *Tlu* = terrestrial low urgency, *Rlu* = recruitment low urgency, *Ahu* = aerial high urgency, *Rhu* = recruitment high urgency. The outer lines in A and B represent contour lines around all data points classified to each call type.

$P = .002$ ). Moreover, for recruitment calls, male young already had scores equal to those of adult males, whereas there was a clear difference between young and adult females (age  $\times$  sex:  $F = 10.45$ ,  $df = 1, 18$ ,  $P = .005$ ). For terrestrial calls, young emitted calls with both higher peak frequency and more energy located at higher frequencies compared with adults.

Calls of adults and young also differed in the scores of the second principal component for aerial and terrestrial

calls but not recruitment calls (aerial:  $F = 4.97$ ,  $df = 1, 92$ ,  $P = .03$ ; terrestrial:  $F = 14.51$ ,  $df = 1, 13$ ,  $P = .002$ ; recruitment:  $F = 1.20$ ,  $df = 1, 18$ ,  $P = .29$ ). For aerial calls, individuals younger than 6 months had a little more modulated and longer calls compared with subadults and adults. After 6 months, calls showed little change regarding modulation and duration. For terrestrial calls, young exhibited a lower amplitude ratio between the first and second dominant frequency bands, which was much

**Table 2:** Effect of age on each of the principal components (PC) included in the univariate analysis of each call type

Call type	PC1	PC2	PC3	PC4	PC5
Aerial low urgency	+	+	+	0	0
Terrestrial low urgency	+	+	0	0	0
Recruitment low urgency	+	0	0	0	0
Aerial high urgency	0	0	0	0	0
Recruitment high urgency	+	0	0	0	0

Note: Plus sign represents change with age, and 0 represents no change.

more apparent in males than females (age  $\times$  sex:  $F = 21.18$ ,  $df = 1, 13$ ,  $P < .001$ ). The third principal component was influenced by age for aerial calls ( $F = 11.50$ ,  $df = 1, 92$ ,  $P = .001$ ) but not terrestrial ( $F = 0.89$ ,  $df = 1, 22$ ,  $P = .35$ ) or recruitment calls ( $F = 1.01$ ,  $df = 1, 18$ ,  $P = .32$ ). Young  $< 6$  months of age had, as for terrestrial calls, more energy at higher frequencies and slightly more noisy calls compared with adults. Remaining components were not influenced by age for any call type ( $P > .10$  for all). Apart from the above-mentioned effects, there was no influence of sex on any of the other principal components ( $P > .20$  for all call types).

In contrast to calls emitted in low-urgency contexts, we found very little effect of age on calls emitted in high-urgency contexts. None of the principal component scores for aerial high-urgency calls were influenced by age (PC1:  $F = 0.69$ ,  $df = 1, 17$ ,  $P = .42$ ; PC2:  $F = 0.62$ ,  $df = 1, 17$ ,  $P = .44$ ; PC3:  $F = 0.34$ ,  $df = 1, 17$ ,  $P = .57$ ; PC4:  $F = 0.61$ ,  $df = 1, 17$ ,  $P = .45$ ; table 2), and for recruitment high-urgency calls, only the first component was affected (PC1:  $F = 20.88$ ,  $df = 1, 27$ ,  $P < .001$ ; PC2:  $F = 0.42$ ,  $df = 1, 27$ ,  $P = .52$ ; PC3:  $F = 0.03$ ,  $df = 1, 18$ ,  $P = .86$ ; PC4:  $F = 0.60$ ,  $df = 1, 27$ ,  $P = .45$ ; table 2). Young again had more energy located at higher frequencies and higher median peak frequency than adults. There was no influence of sex on any of the components ( $P > .12$  for both call types).

## Discussion

The alarm calls of young meerkats were more or less structurally indistinguishable from those of adult calls when first produced, yet the discrimination of calls along the level of urgency was better than the discrimination of different predator types. Calls of both adults and young showed a high correct classification to low-urgency (predators far away) and high-urgency (predators close by) contexts and a consistent change in acoustic structure along the level of urgency across predator types (for adult calls, see also Manser 2001). In contrast, whereas predator-specific calls given by adults showed a high correct classification, those given by young overlapped more and

showed a correct assignment similar to that expected by chance. These results suggest that the adultlike structure of acoustic features encoding information about the level of urgency develops earlier than the structure of those features encoding information about specific predator types.

Since acoustic parameters encoding information about the level of urgency in meerkat alarm calls (see Manser 2001) are all features known to be associated with fear or anxiety in other animal vocalizations and human speech (Morton 1977; Papoušek 1989; Hauser 1993), it is reasonable to assume that the acoustic structure grading along the level of urgency may be a direct consequence of the caller's motivational state at the time of calling (Morton 1977; Marler et al. 1992; Evans 1997). Because meerkat alarm calls seem to convey information about the level of urgency along a general rule, in contrast to the information about specific predator types (Manser 2001; this study), it has been suggested (Manser 2001) that such an alarm call system might support the idea that motivational signals are the substrate from which referential signals evolve (Macedonia 1993). Our results showing that referential aspects of alarm calls change more over time provide additional support for this idea. Moreover, the high-urgency growl calls emitted by very young pups clustered relatively separately from other high-urgency predator-specific calls, suggesting that growl calls gradually develop into the other call types as young grow older. We also previously found that predator-specific calls appear much later in the repertoire of young than do nonspecific calls (L. I. Hollén and M. B. Manser, unpublished data). Together, these findings suggest that producing and correctly pronouncing calls encoding referential information may require practice, and they show similarities to that observed in human speech development, where children learn to attach specific meanings to different words (Locke and Snow 1997).

Although the calls of young showed relatively little discrimination between the different predator types, they were classified slightly better in high-urgency than in low-urgency contexts. Compared with low-urgency calls, high-urgency calls also showed a high correct classification when the principal components explaining differences between adult calls were used to assign the calls of young and vice versa, suggesting that the structure of high-urgency calls is already similar to that of adult calls. This was confirmed by the univariate analysis showing that high-urgency calls underwent relatively little age-related modification. A similar pattern was found in ring-tailed lemurs (*Lemur catta*), where aggressive calls typically noisy in structure, whether present or not at birth, were relatively adultlike in structure when they appeared in the repertoire (Macedonia 1993). One explanation for these findings could be that noisy calls are easier for young individuals to produce than are



tonal calls, since they require relatively little control over the vocal apparatus (e.g., Lieberman 1986). It has been suggested that in humans, an age-related increase in tonality of infant calls is likely to be brought about by an improvement of the subglottal air pressure control as individuals grow (Boliek et al. 1996; Scheiner et al. 2002).

Our univariate analysis showed that the alarm calls of meerkats undergo slight but not substantial modification as individuals age, a form of vocal plasticity found in several other species. The calls of young meerkats were higher pitched than those of adults, similar to infant primates (e.g., Seyfarth and Cheney 1986; Gouzoules and Gouzoules 1989; Hammerschmidt et al. 1994, 2000), young rodents (Blumstein and Munos 2005; Randall et al. 2005), and human children (Scheiner et al. 2002). Changes in fundamental and peak frequency-related parameters determining the pitch are likely to reflect physical maturation because of the increasing length of the vocal tract and the size of the resonance cavities as individuals age and grow (Fitch and Hauser 1995; Fischer et al. 2002). Why young males, in contrast to females, emitted calls of equally low frequencies as those of adults remains unclear at this stage. Similar maturational changes may be responsible for the increase in amplitude of the first dominant frequency band relative to that of the second band and the downward shift of the main energy from higher to lower frequencies with increasing age. In human infants, however, an increase in fundamental frequency (Banse and Scherer 1996; Protopoulos and Lieberman 1997), an increase in call duration, and an upward shift in energy from lower to higher frequencies (Scheiner et al. 2002) were also found during increased arousal. If young meerkats, because of their higher vulnerability, experience higher arousal than adults at the time of an alarm call, this might be responsible for some of the observed differences. However, this remains to be investigated.

To conclude, young meerkats seem predisposed to utter alarm calls with the same general features as those of adults from an early age but nevertheless undergo gradual modification during development. Adultlike features related to predator-specific information seem to develop at later ages than those encoding information about perceived urgency. The developmental trajectories of alarm call production found in meerkats extend the already existing parallels between the properties of speech development in humans and the development of call production in many nonhuman primates. To our knowledge, however, this is the first study on nonhuman animals to consider the specific information conveyed by different alarm calls when studying their development.

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