

ACOUSTIC CHARACTERISTICS OF WHITE-NOSED COATI VOCALIZATIONS: A TEST OF MOTIVATION-STRUCTURAL RULES

L. A. COMPTON, J. A. CLARKE,* J. SEIDENSTICKER, AND D. R. INGRISANO

*Department of Biological Sciences, University of Northern Colorado, 501 20th Street,
Greeley, CO 80639 (LAC, JAC)*

National Zoological Park, Smithsonian Institution, Washington, DC 20008 (JS)

*Department of Communication Disorders, University of Northern Colorado, 501 20th Street,
Greeley, CO 80639 (DRI)*

Vocalizations of white-nosed coatis (*Nasua narica*) emitted in nonaggressive and aggressive contexts were measured and compared to determine if these calls exhibited acoustic characteristics in accordance with motivation-structural (MS) rules. “Chirp” and “squawk” calls were compared spectrographically using 11 coatis from 3 zoos. Chirps were short-duration (68.6–212.0 ms), high–maximum frequency (16.2–17.9 kHz), tonal calls with frequency modulations. Squawks were longer-duration (177.9–546.5 ms), low–maximum frequency (8.4–13.2 kHz), wide-bandwidth calls with 6 resonances and little frequency modulation. Squawks differed from chirps in duration, maximum frequency, and change in frequency ($P < 0.001$). Chirps were emitted during nonaggressive behaviors, whereas squawks were emitted during agonistic encounters. Squawks conformed to MS rule predictions for aggressive calls, and chirps supported MS rule predictions for nonaggressive contexts, but some exceptional characteristics were noted in chirps. Many chirps (67.7%) concluded with a short-duration, broad-bandwidth sound with high energy in low frequencies, and may represent variations of a graded call.

Key words: motivation-structural rules, *Nasua narica*, vocalizations, white-nosed coati

Motivation-structural (MS) rules proposed by Morton (1977) generalize that vocalizations emitted by mammals and birds in hostile contexts are low-frequency (low pitch), wide-bandwidth (noisy) sounds, whereas vocalizations emitted in fearful or appeasement contexts are high-frequency (high pitch), narrow-bandwidth (tonal) sounds. MS rules are based on the hypothesis that natural selection may favor the use of harsh, low-frequency vocalizations in conflict situations because such sounds are linked to large body size, which often influences the outcome of aggressive interactions. Conversely, selection would favor the use of tonal, high-frequency vocalizations in fearful and friendly contexts because these sounds symbolize

smaller size or juvenile age class, thus reducing the likelihood of attack by the receiver of the call (Morton 1977; Owings and Morton 1998). August and Anderson (1987) tested the applicability of MS rules using data from studies of vocalizations of 50 mammalian species, and found that calls emitted in aggressive situations supported MS rule predictions. However, mammalian vocalizations emitted in fearful or appeasement (friendly) contexts were not in complete accordance with MS rules, perhaps because pooling of fearful calls with appeasement calls introduced variation due to their different motivations (August and Anderson 1987).

Our goal was to measure and compare white-nosed coati (*Nasua narica*) vocalizations emitted in aggressive and nonaggressive

* Correspondent: jaclarke@unco.edu

sive contexts and to test the hypothesis that these calls exhibited acoustic characteristics in accordance with MS rules (Morton 1977). The white-nosed coati is native to Central America, Mexico, and Southwestern United States (Kaufmann et al. 1976; Taber 1940). Coatis (*Nasua*) are ideal for studies of vocalization complexity because, with the exception of being diurnal instead of nocturnal, they meet 3 of the 4 criteria that predict the use of extensive vocal communication (Kiley-Worthington 1984). Specifically, coatis are a social species that travel in groups (Gilbert 1973; Kaufmann 1962), live in forest habitats (Gilbert 1973; Kaufmann 1962; Kaufmann et al. 1976; Taber 1940), and have relatively extended mother-infant contact (Gompper 1995). Furthermore, studies have reported that coatis emit audibly different calls in contexts ranging from friendly to agonistic encounters (Gilbert 1973; Kaufmann 1962; Smith 1980). We compared chirp vocalization, a contact call with signature characteristics (Maurello et al. 2000), with squawk vocalization which is often emitted during fights.

MATERIALS AND METHODS

We recorded vocalizations of 5 female and 6 male white-nosed coatis from 5 different groups of coatis at 3 zoos in the United States. All recordings of vocalizations were made in the animals' outdoor enclosures. Three female coatis and 4 male coatis used in this study were from Smithsonian National Zoological Park (Washington, D.C.). Six of those coatis were born at Smithsonian National Zoological Park, and 1 male was born at Denver Zoo (Denver, Colorado). One female and 2 males used in this study were housed together at Phoenix Zoological Park (Phoenix, Arizona). The female was born at Fossil Rim Wildlife Center (Glen Rose, Texas), 1 male was born at the Denver Zoo, and 1 male was wild born (Arizona). Vocalizations of a wild-born female (housed with a male and female brown-nosed coati, *N. nasua*) were also recorded at Wildlife World Zoo (Glendale, Arizona).

We recorded vocalizations with a Sony TC-D5PROII tape recorder (frequency response, 40–15,000 Hz; speed, 1.88 inches/s; Sony Corporation, Tokyo, Japan) and a Sennheiser ME 66 mi-

crophone (frequency response, 40–20,000 Hz; Sennheiser Electronics, Wedemark, Germany). Vocalizations were recorded on Maxell XL II 60 High Bias IEC Type II audio tapes (Maxell Corporation, Conyers, Georgia). Recordings were collected within ≤ 3 m of each individual while they were in their outdoor enclosures, except for those at Phoenix Zoological Park, which were recorded indoors. We collected recordings during the morning (0630–1100 h), midday (1100–1500 h), and late afternoon (1500–2000 h). We recorded vocalizations of each animal for ≥ 5 days and during each daily time period from 4 June to 25 July 1997.

The nonaggressive call recorded was labeled "chirp" because the measured acoustic variables of that call did not differ (Mann-Whitney *U*-test, $n = 40$, $P > 0.05$, in all cases) from those of the chirp calls quantitatively described by Maurello et al. (2000). The aggressive call recorded was labeled "squawk" because, although aggressive calls have been noted in other studies of coati vocalizations (Gilbert 1973; Kaufmann 1962; Smith 1980), those calls were identified by auditory means alone (grunt, squeal, chitter, growl, chop-chop), and we could not determine if we were hearing a previously described call because of differences in human auditory discrimination.

Behaviors of coatis immediately before and after each call were used to classify the call context into 3 categories (Smith 1980). In the 1st category are the relaxed behaviors of foraging, allogrooming, playing with conspecifics, and resting. In the 2nd category are the nervous behaviors when investigating unfamiliar objects or people and exhibiting exaggerated rigid body posture in response to unfamiliar stimuli. Agonistic behaviors when engaged in threat displays and fighting belong to the 3rd category. Eighty-seven best-quality (low noise) recordings were used to determine if a call was emitted in a non-aggressive (relaxed and nervous) or aggressive (threatening and fighting) situation. Original recordings will be housed at Cornell Library of Natural Sounds (Ithaca, New York).

Because squawks were seldom emitted, and chirps were frequently emitted, the 10 best-quality squawks (from 10 individuals) and 20 best-quality chirps (≥ 1 chirp from each individual) were digitized and analyzed using Canary software version 1.2.1 (Canary Institute, Inc. 1995). In order to digitize and create spectrograms, we used an analysis window of 5 ms, a sampling

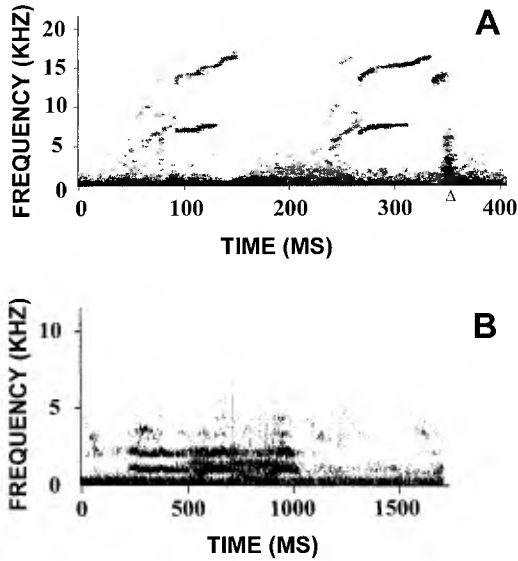


FIG. 1.—Spectrograms of chirp and squawk vocalizations of white-nosed coatis: A) 2 chirps of a male coati, 1 without and 1 with a concluding plosive (Δ), and B) squawk of a female coati.

rate of 44.1 kHz with 16-bit precision, a short-time Fourier transform math model of 256 points, and a broad-band filter spectrogram of 699.40 Hz with a frame length of 256 points. Grid resolution was 2.902 ms with 50% overlap and 172.3 Hz. A Hamming window was used for filtering.

Spectral display examination revealed if the calls consisted of primarily steady-state frequencies or dynamic changes in frequency, and slopes of modulated frequency bands were determined (Δ kHz/ Δ ms). Calls were also examined for the presence of continuant energy (extended sound) or transient energy (brief burst of sound).

Acoustic characteristics measured were duration of the call (ms), maximum frequency (kHz), and change in frequency (kHz) over the entire call. Intensity (loudness) was not measured be-

cause coatis moved about in their enclosures and their distance from the microphone varied. Differences in the measured variables were examined using nonparametric statistics (SAS Institute Inc. 1988) because data did not exhibit a normal distribution (Shapiro-Wilks test, $P < 0.05$). Pairwise comparisons were made using Mann-Whitney U -tests (Siegel and Castellan 1988) to determine where differences existed between squawk and chirp calls in duration, maximum frequency, and change in frequency. In all cases, significance was set at $P \leq 0.05$.

RESULTS

Chirp calls were emitted often by all individuals and were typically difficult to hear because they were high pitched and had an extremely short duration (Fig. 1; Table 1). Chirps were characterized by initial up-sweeping modulations (increasing from low to high kilohertz), frequency modulations (termed on-glides) in the 1st bar (slope range = 0.07–0.26 kHz/ms, \bar{X} duration = 38 ms) and 2nd bar (slope range = 0.05–0.19 kHz/ms). These initial on-glides were followed by steady-state to slightly modulated frequencies (\bar{X} duration = 70 ms). A short-duration, low-frequency (<10 kHz) burst of energy (termed plosive) was present at the conclusion of 67% (42/62) of chirp calls. Most of the chirp calls examined (74%, 46/62) were recorded while coatis were moving around their enclosures and foraging, or while they were allogrooming (relaxed conditions). Twenty-three percent (14/62) of chirp calls were emitted when coatis were investigating unusual objects or people (potentially nervous conditions). Two chirps (3%, 2/62) were emitted before an agonistic conflict, but they were immediately followed by squawks.

Squawk calls sounded loud, noisy, and

TABLE 1.—Median (and ranges) of duration, high frequency, and change in frequency of chirp ($n = 20$) and squawk ($n = 10$) vocalizations of white-nosed coatis.

Call	Duration (ms)	High frequency (kHz)	Change in frequency (kHz)
Chirp	106.0 (68.8–212.0)	17.0 (16.1–17.9)	12.6 (9.0–14.6)
Squawk	222.0 (177.9–546.5)	9.0 (7.8–13.2)	8.0 (6.9–9.7)

harsh, relative to chirp calls (Fig. 1; Table 1). Duration of squawks (range = 117.9–546.5 ms) was greater than duration of chirps ($z = 4.0259$, $P < 0.01$), and maximum frequency of squawks (range = 8.4–13.2 kHz) was lower than maximum frequency of chirps ($z = -4.3882$, $P < 0.01$). Change in frequency of squawks (range = 6.9–9.7 kHz) was less than that of chirps ($z = -4.3383$, $P < 0.01$). All components of the squawk were steady-state resonances (lacking distinct frequency modulations) and contained 6 resonance bars (range = 1.21–7.09 kHz). All squawks recorded (100%, 25/25) were emitted during agonistic intraspecific encounters. Coatis in all populations occasionally engaged in physical fights.

DISCUSSION

Coatis are highly social mammals that use vocal signals in a variety of situations. These range from maintaining auditory contact between group members while traveling through dense vegetation to agonistic interactions. We determined that the acoustic structure and context of the squawk call fully conformed to Morton's MS rules for an aggressive signal (Morton 1977). The chirp call conformed to MS-rule predictions for nonaggressive vocalizations, but with some variation. This was compatible with the findings of August and Anderson (1987) for a number of mammalian species.

Chirp calls, which function as contact calls (Maurello et al. 2000), were high-frequency tonal sounds, emitted in nonaggressive contexts. Morton (1977) pooled animal sounds made in fearful and appeasement (friendly) situations into a nonaggressive category of sounds. Although fear and friendliness are different from hostility (aggression), they also are distinct from one another (August and Anderson 1987). Chirp calls of coatis supported MS-rule predictions in general for fearful or appeasement calls, but 1 call component exhibited characteristics predicted for an aggressive call. The majority of chirps (67%) concluded with a plosive, a short-duration energy burst of low

frequency. These plosives were not unique to individuals (an individual may emit a chirp without a plosive and later emit a chirp with a plosive). In avian signaling, plosives are associated with the need for immediate close attentiveness from others (Marler 1967), and this plosive may be included in the coatis' calls when communicating urgency. However, such "alerting" components are most often at the beginning of a call instead of at the conclusion. Chirps with and without a concluding plosive may represent graded variations of the call. Graded vocalizations may serve as high information signals (Miller and Baker 1980) and, in this case, could represent contexts that were neither entirely fearful nor entirely relaxed and friendly but were combinations of these motivations. Graded calls are also used more frequently over short distances than long distances (Marler 1967), as were the chirp calls of coatis (Maurello et al. 2000).

Coatis and raccoons, *Procyon lotor*, are closely related, and coati chirp calls appear similar to the "tonal" calls of raccoons (Sieber 1983, 1986). Raccoon tonal calls have narrow-frequency bands and contain two call types with a large overlap in frequency components, similar to chirps with and without plosives. Tonal calls of raccoons appear to be emitted more often in fearful contexts and exhibit individual variation (Sieber 1983, 1986), whereas chirps of coatis were emitted more in friendly contexts, but, as revealed in our previous study, chirps also exhibited individual variation (Maurello et al. 2000). Squawk calls of coatis may be similar to the "mixed" calls of raccoons that are also described as noisy, lower-frequency calls used in aggressive contexts (Sieber 1983).

August and Anderson (1987) noted that MS rules represent only 1 level of selection on the design of animal vocalizations and that, in order to address the reason why a sound has particular acoustic characteristics, other possible selective pressures must be considered. These may include the ability to be localized and factors related to attenua-

tion and distortion. Considering the design of chirps, the initial up-sweeping energy in chirps was similar to the rapid rise time evident in avian calls where localizing by conspecifics is at a premium (Marler 1967). The high-frequency and short-duration characteristics of chirp calls appear advantageous in maintaining contact with nearby group members because the call would attenuate before reaching more distant potential predators (Maurello et al. 2000). Graded variations in chirps may provide fine-grained information regarding the motivation or behavioral context of the sender. The form of squawks may be less complex because this call was used in face-to-face confrontations where visual and olfactory signals were also present, and because the message was unequivocal. The atonal energy pattern present in squawks, also present in aggressive vocalizations of other species of mammals and birds, has been proposed to be related to the simplicity of the acoustic message (Morton 1977).

Our study illustrated the complex nature of a subset of vocalizations of white-nosed coatis, supporting MS-rule predictions (Morton 1977) and findings that nonaggressive calls exhibit more exceptions to the rule (August and Anderson 1987). However, we did not test a primary assumption of Morton's MS rules (Morton 1977). Studies are needed to elucidate if mammals associate low-frequency sounds with large body size and a greater threat and high-frequency sounds with smaller body size and lower threat.

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