

## Hearing and Vocalizations in the Orange-Fronted Conure (*Aratinga canicularis*)

Timothy F. Wright  
University of Maryland

Kathryn A. Cortopassi and Jack W. Bradbury  
Cornell Laboratory of Ornithology

Robert J. Dooling  
University of Maryland

The auditory sensitivities of the orange-fronted conure (*Aratinga canicularis*) were examined in relation to the spectral characteristics of its vocalizations. Absolute thresholds, masked thresholds, frequency difference limens, and intensity difference limens for pure tones were obtained using psychoacoustic techniques. In general, hearing abilities are similar to those found in many avian auditory generalists. One exception is the unusually low critical ratio (masked threshold) between 2.0 and 4.0 kHz, similar to that previously found in the budgerigar (*Melopsittacus undulatus*). These auditory sensitivities were compared with average spectra for (a) contact calls and (b) a general sample of vocalizations recorded from wild birds. The spectral regions of both greatest vocal energy and best auditory sensitivity were between 2.0 and 5.0 kHz.

The need to detect and discriminate among conspecific communication signals may have played an important role in the evolution of the avian auditory system (Klump, 1996; Webster, Popper, & Fay, 1992; Wiley & Richards, 1978). The acoustic structure of a communication signal is probably influenced by a variety of factors, including its production costs and communication function, the body size and evolutionary history of the signaling species, and the ambient noise and frequency-dependent transmission characteristics of the environment through which the signal must propagate (Morton, 1975; Ryan, 1986; Ryan & Brenowitz, 1985; Wiley & Richards, 1978). Hearing abilities may likewise be constrained by the evolutionary history of a species (Webster et al., 1992) and by the physiological challenge of preserving both the temporal and spectral characteristics of a communication signal (Cortopassi & Lewis, 1998; Lewis, 1987). Absent these constraints, one might predict a close correspondence between the acoustic characteristics

of a species' communication signals and the spectral and temporal sensitivities of its auditory system so as to enhance the transfer of information in these signals. Documenting the degree to which this correspondence exists is an important first step to understanding the relative influence of these potential constraints on evolution. One approach to understanding the relationship between signal production and reception abilities is to compare data from controlled psychoacoustic studies of hearing with measurements of natural variation in vocal communication signals (e.g., Brenowitz, 1982; Dooling, Mulligan, & Miller, 1971; Dooling, Peters, & Searcy, 1979; Dooling & Saunders, 1975b; Dooling, Zoloth, & Baylis, 1978; Hienz & Sachs, 1987).

Studies of the budgerigar (*Melopsittacus undulatus*) provide one of the best examples of the utility of this approach. This small (30 g) Australian parrot has been the subject of numerous studies of hearing and vocal communication (reviewed in Dooling, 1982, 1986; Dooling, Lohr, & Dent, 2000; Farabaugh & Dooling, 1996). The most common call in this species' vocal repertoire is its contact call, a short frequency-modulated call with spectral energy concentrated between 2.0 and 4.0 kHz (Dooling, 1986). Budgerigars exhibit thresholds for pure tones presented in the quiet that are generally low, between 0.5 and 5.0 kHz, with a region of best sensitivity between 2.0 and 4.0 kHz (Dooling, 1982, 1986). Although this frequency range corresponds well to the peak spectral energy of the budgerigar's contact call, the overall shape and general sensitivity of the budgerigar audiogram is similar to that found for a wide range of bird species (Dooling et al., 2000).

*Absolute thresholds*, also termed *audibility curves* or *audiograms*, measure the lowest level of a tone a species can detect in the quiet over a range of frequencies. Other auditory measures that may be relevant for the perception of communication signals include thresholds for detecting tones in the presence of masking noise (*masked absolute thresholds*) and for discriminating small

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Timothy F. Wright and Robert J. Dooling, Department of Psychology, University of Maryland; Kathryn A. Cortopassi and Jack W. Bradbury, Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology.

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Correspondence concerning this article should be addressed to Timothy F. Wright, who is now at the Molecular Genetics Laboratory, Smithsonian National Zoo, 3001 Connecticut Avenue, Washington, DC 20008. E-mail: tw98@umail.umd.edu

differences in frequency and intensity (*difference limens*). The signal-to-noise ratio at the threshold of detection for a tone embedded in masking noise is termed the *critical ratio*, and it may provide a measure of spectral resolving power. Smaller critical ratios suggest smaller frequency bandwidths and, therefore, greater frequency selectivity within the auditory system (Dooling & Searcy, 1979). Critical ratios for the budgerigar are lowest in the range of 2.0–4.0 kHz. This pattern contrasts with that typically observed in birds and mammals, in which the critical ratio shows an increase in signal-to-noise ratio of 2–3 dB per octave increase in frequency over the range of hearing (Dooling et al., 2000; Klump, 1996; Okanoya & Dooling, 1987). The region of small critical ratios in budgerigars corresponds to the region containing most of the spectral energy of the budgerigar contact call, suggesting the presence of species-specific adaptations for perceiving these calls.

The minimum discriminable frequency difference between two pure tones is termed the *frequency difference limen* (FDL); similarly, the minimal discriminable difference in intensity between two tones is the *intensity difference limen* (IDL). Both measures give further indication of the resolving power of the auditory system over the range of hearing. FDLs for budgerigars are also smallest between 2.0 and 4.0 kHz (Dooling & Saunders, 1975b), and call discrimination tests indicate that budgerigars are better able to discriminate among sets of conspecific contact calls than among sets of calls from other species (Dooling, Brown, Klump, & Okanoya, 1992). To date, the physiological basis of these enhanced abilities remains unidentified (Manley, Schwabedissen, & Gleich, 1993).

It remains an open question whether these auditory abilities of the budgerigar represent an evolved adaptation for processing species-specific vocalizations. One way to address this issue is to evaluate whether other species of parrots show a similar relation between vocal characteristics and hearing abilities. A study by Okanoya and Dooling (1987) compared audiograms and critical ratio functions of single representatives of seven species of small birds, including the cockatiel (*Nymphicus hollandicus*), a small (100 g) Australian parrot. The cockatiel had an audiogram similar in shape and overall sensitivity to that of the budgerigar (Okanoya & Dooling, 1987). The cockatiel critical ratio function, however, did not show an area of unusually low signal-to-noise ratio as found in budgerigars (Okanoya & Dooling, 1987). Intriguingly, these two parrot species may also differ in the acoustic form of their contact call. Budgerigar contact calls are short calls (~200 ms) with rapid frequency modulation and a concentration of spectral energy between 2.0 and 4.0 kHz (Dooling, 1986). In contrast, cockatiel contact calls are longer (~800 ms), with little frequency modulation and a broadband spread of spectral energy in many harmonic overtones (Zann, 1965). These differences suggest that there may be a relationship between contact call acoustic structure and the shape of the critical ratio function in parrots. One rationale for the present study is to examine contact call structure and hearing abilities in a third parrot species from a different phylogenetic lineage to test the generality of this hypothesis.

The orange-fronted conure (*Aratinga canicularis*) is a small (70 g) Neotropical parrot found in the seasonal dry forest of the Pacific slope of Central America. Neotropical and Australasian parrots are generally thought to comprise two separate independent radiations representing monophyletic clades with respect to each other

(Brown & Toft, 1999; Forshaw, 1989; Miyaki, Matioli, Burke, & Wajntal, 1998). Thus the Neotropical orange-fronted conure is more distantly related to the Australian budgerigar and cockatiel than either of those species are to each other and represents an independent evolutionary contrast relative to the two Australian species. Like many parrots, including the budgerigar and cockatiel, the orange-fronted conure is highly social with both foraging and roosting occurring in flocks (Bradbury, Cortopassi, & Clemmons, 2001; Hardy, 1963). Orange-fronted conures produce a variety of different calls, of which the most common are the contact (or *chee*) call (see Figure 1), the *peach* call, and the *zip* call (Bradbury & Cortopassi, 2000; Hardy, 1963). In Costa Rican populations, the contact call is both the most commonly used call and the loudest, with typical levels of 90–95 dB sound pressure level (SPL) measured at 1 m (Bradbury et al., 2001). Typical contact calls are about 200 ms in length and can be divided into three segments: an initial harmonic segment with a rising fundamental, a central segment with a higher fundamental and stepwise frequency modulation, and a terminal segment of harmonics with a descending fundamental (Cortopassi & Bradbury, 2000). This three-part structure is conserved throughout the geographic range of this species, with calls from Mexico containing the same basic elements as calls from Costa Rica (Bradbury & Cortopassi, 2000). Within the Costa Rica populations, contact calls do exhibit fine-scale variation both geographically and among individuals, with each bird having a dominant call version that differs from those of other birds in the same flock (Bradbury et al., 2001; Cortopassi & Bradbury, 2000). Such fine-scale variation suggests that contact calls may be used to discriminate among and identify both individuals and higher social groupings. It is likely that performing such discriminations efficiently and accurately could confer a selective advantage on individuals. Thus the ability to perform such auditory tasks may have been an important selective force in the evolution of orange-fronted conure hearing abilities.

Here we compare spectral characteristics of the vocal repertoire of the orange-fronted conure to several measurements of hearing sensitivity obtained through psychoacoustic testing using operant conditioning techniques. We find generally close correspondence between the spectral characteristics of these calls and the regions of best sensitivity for absolute thresholds, masked auditory thresholds, FDLs, and IDLs.

## Spectral Characteristics of Vocalizations

### Method

We used two methods to assess the overall frequency characteristics of vocalizations produced by orange-fronted conures (*Aratinga canicularis*) in the wild. First, we measured spectral power distribution on the total power spectra from individual contact calls and averaged these measures. Second, we measured the average spectral power distribution function for a general sample of vocalizations recorded at the night roost, a highly social and vocally rich context. For this general vocal sample, contact call vocalizations were specifically excluded.

For the contact call-specific analysis, a sample of 288 contact calls was taken from recordings made of 8 wild-caught birds held in captivity during the period from July 21, 1997, to August 8, 1997. A spectrographic cross-correlation and principal coordinates analysis of these calls has been presented elsewhere (Bradbury et al., 2001). The birds were mist-netted at foraging sites in the Area de Conservación Guanacaste (ACG) of northwest

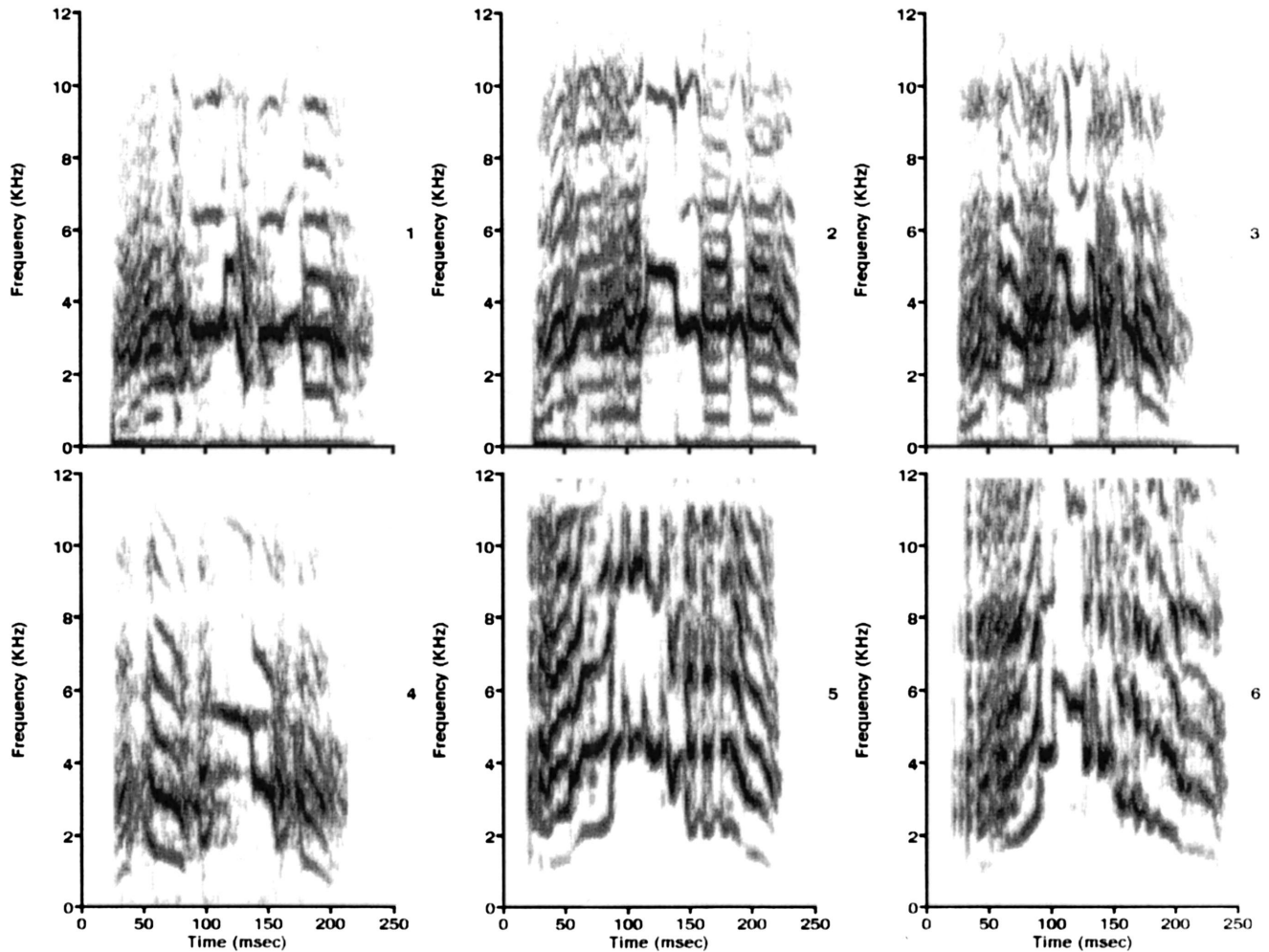


Figure 1. Spectrograms of representative contact calls from 4 wild orange-fronted conures (Spectrograms 1–4) and 2 of the captive-bred conures used as subjects in this study (Spectrograms 5–6). msec = milliseconds.

Costa Rica and held captive in an outdoor aviary. Each bird was held for no longer than 12 days total, and no more than 4 birds occupied the aviary at one time.

Video and audio recordings were made using a Hi8 video camcorder (Canon model ES2000, Lake Success, NY) and a directional microphone (Sennheiser model MKH 816 P48, Wedemark, Germany) powered by a phantom supply (Stewart Electronics model BPS-1, Columbia, CA). In total, 288 contact calls were identified to caller and digitally acquired on a personal computer using RTS Version 2.0 (Engineering Design, Belmont, MA). The combined duration of the calls was 57 s. Calls were sampled at 40,000 points per second, and bandpass filtered from 80 to 16000 Hz (Krohn-Hite model 3550 filter, Brockton, MA) before acquisition to prevent aliasing. A detailed frequency analysis was performed using Signal Version 3.1 (Engineering Design). Any direct current bias was removed, and frequency spectra (as power spectral density functions) were generated for each of the 288 contact calls using a 32,000-point fast Fourier transform (FFT) and a Hanning window function. A 75-point running average was applied (on linear amplitude values) to smooth the individual spectra. We measured the following frequency parameters for each spectrum: the frequency at the spectral amplitude peak (peak frequency), the  $-12$  dB corner below the peak frequency (low-frequency corner), the  $-12$  dB corner above the peak frequency (high-frequency corner), and the corre-

sponding  $-12$  dB bandwidth and its center frequency (linear and log). The low- and high-frequency corners were estimated by gating the spectra between 0.25 and 12.0 kHz with a threshold value set to 12 dB below their peak values and a minimum peak detection width of 100 Hz. Signal bandwidth is commonly measured between  $-3$  or  $-6$  dB corners, which represent the half-power and half-amplitude cutoffs, respectively; here we measured the  $-12$  dB corners as this level may include biologically relevant acoustic energy. We also generated an average spectrum for the 288 contact calls by ranging linear amplitude values to a peak value of 1 and then summing and averaging the resulting spectra.

For the general vocalization analysis, a sample of vocalizations was taken from recordings made of roughly 60 wild orange-fronted conures observed at a night roost in the ACG. Continuous recording of all vocal activity by the group was made from 1645 to 1715 central standard time (roughly 40–70 minutes before sunset) on June 5, 2000, at the beginning of the nonbreeding season for this species. The birds were gathered in a large bare tree in small groups of 1–4 birds, with most birds sitting in pairs. During this time, birds preened themselves and others and displayed a wide variety of other typical late-afternoon behaviors. In addition, several pairs and small groups flew into the area and joined the large assemblage already present in the tree. This staging phase that occurs prior to roosting is a highly social and vocally rich period in which one is likely to hear



renditions of most of the vocalizations in this species' repertoire. Thus, we felt that this was the most appropriate occasion to collect a representative sample of the vocal repertoire.

Video and audio recordings were made, and sounds were digitally acquired and spectrally analyzed using the equipment and specifications described above (except that here RTS Version 2.1 was used for sound acquisition). Sound segments used in the analysis consisted of either single isolated vocalizations or sequences of continuous vocalizing, often from multiple birds calling simultaneously. No attempt was made to determine caller identity. We excluded sound segments that contained contact calls or background noise (consisting primarily of wind, highway noise, insects sounds, and to a lesser degree, heterospecific avian vocalizations); all other segments were used in the analysis. Segments with contact calls were excluded because their high frequency of use could have heavily biased the acoustic measurements. In all, 129 sound segments were pulled from the night-roost staging recording with durations ranging from 93 to 4,241 ms (total duration of sound analyzed was 87 s). A long-term average spectrum (i.e., power spectral density function) was then generated for each of the 129 night-roost segments. Specifically, for long duration segments, a 32,000-point FFT was applied to the sound sequentially and the resulting spectra were summed and averaged. Similarly, for short duration segments, a single 32,000-point FFT was applied. The resulting 129 spectra were then summed and averaged. In this case, to simulate the calculation of a long-term average, we did not adjust the individual spectra to have a peak value of 1 before being summed. The frequency parameters described above for contact call spectra were measured for this long-term average spectrum.

### Results and Discussion

The spectra calculated from the 288 contact calls recorded from 8 wild-caught conures showed the following spectral features: mean peak frequency = 3351 Hz ( $SD = 283$ ); mean  $-12$  dB low-frequency corner = 2778 Hz ( $SD = 315$ ); mean  $-12$  dB high-frequency corner = 4319 Hz ( $SD = 750$ ); mean  $-12$  dB bandwidth = 1541 Hz ( $SD = 862$ ); mean linear band center = 3548 Hz ( $SD = 381$ ); and mean log band center = 3442 Hz ( $SD = 333$ ). An average spectrum calculated from these 288 calls is shown in Figure 2A.

The long-term average spectrum calculated from the segments taken from the night roost staging recordings (see Figure 2B) showed the following spectral features: peak frequency = 2820 Hz;  $-12$  dB low-frequency corner = 826 Hz;  $-12$  dB high-frequency corner = 7000 Hz;  $-12$  dB bandwidth = 6173 Hz (with a band center frequency of 3913 Hz linear and 2405 Hz log).

The average spectrum for contact calls analysis shows  $-12$  dB bandwidths that fall predominantly in the 2.0–5.0 kHz range with both peak frequency and band center frequencies around 3.4 kHz. Spectral power for the general sample of vocalizations is spread over a broader range of frequencies than is that for contact calls, with the long-term average spectrum for the general sample showing a  $-12$  dB bandwidth ranging from 0.8 to 7.0 kHz. This larger bandwidth for the general sample is likely because some of these vocalizations are more broadband than contact calls and also because different vocalizations probably had slightly different peak frequencies. However, the peak frequency and band centers of the time-average spectrum of the general vocal sample also fall between 2.8 and 3.6 kHz. Thus for both contact calls and for the vocal repertoire as a whole, peak spectral power tends to occur around 3.0 kHz.

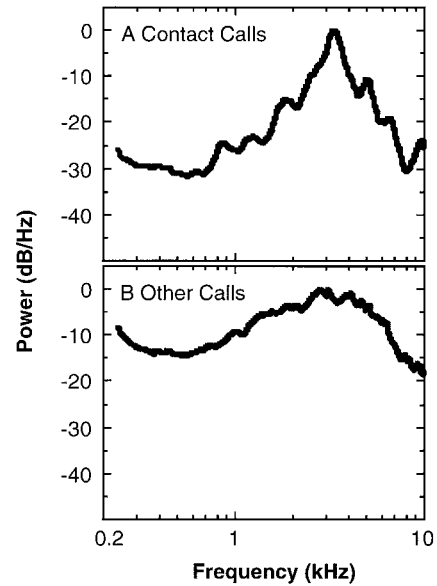


Figure 2. Averaged spectra of 288 contact calls recorded from 8 wild orange-fronted conures held in short-term captivity (A) and of 57 s of general vocalizations (excluding contact calls) taken from 30 min of continuous recording of a wild flock at a night roost in Guanacaste, Costa Rica (B).

### Psychoacoustic Measures of Hearing Sensitivities

#### General Method

**Subjects.** Subjects in the psychophysical experiments were 5 captive-bred orange-fronted conures (*Aratinga canicularis*) obtained from a breeder (D. McInnes, The Animal House, Bryan, TX). These individuals were either second or third generation descendents of wild-caught birds presumably obtained from Mexican populations (D. McInnes, personal communication, July 7, 1999). All birds were obtained and trained 4 months after hatching and ranged in age from 5 to 20 months during the experiments. Birds were housed in individual wire cages and maintained at 90% of free-feeding weight with a controlled diet of budgerigar pellets (Lafeber Co., Cornell, IL) supplemented with a variety of mixed seed, fresh fruits, and vegetables. The birds were kept in a mixed-species vivarium at the University of Maryland in which they had auditory and visual contact with each other and with several other small bird species. The vivarium was maintained on a normal light–dark cycle correlated with the season. Subjects were treated in compliance with American Psychological Association ethical standards, and their use was approved by the Animal Care and Use Committees of the University of Maryland (Protocol 00-93). Five birds were used in Experiment 1, 3 birds were used in Experiment 2, and 2 birds were used in Experiments 3 and 4.

**Apparatus.** The birds were tested in a custom-made operant chamber consisting of an 18 cm  $\times$  27 cm  $\times$  18 cm wire cage with a food hopper and two response keys. Response keys were light-emitting diodes (LEDs) connected to microswitches that were tripped when birds pecked the LEDs. The left LED served as the observation key, and the right LED served as the report key. Behavior of the animal during test sessions was monitored using a video camera (Sony HVW-322, Tokyo, Japan), and the entire apparatus was mounted in a sound isolation chamber (Industrial Acoustics Company, Bronx, NY). Further details of the testing apparatus and procedure are described elsewhere (Dooling & Okanoya, 1995; Okanoya & Dooling, 1988; Park, Okanoya, & Dooling, 1985).

Test sessions and stimulus presentation were controlled by software running on a Pentium microcomputer. Stimuli were generated digitally and

output through Tucker-Davis Technologies (TDT; Alachua, FL) modules to a loudspeaker (KEF model 60s, KEF Electronics, Holliston, MA) mounted 40 cm above the perched bird's head. Tonal stimuli were generated with SIGNAL software (Beeman, 1998) at either a 20.0- or 40.0-kHz sampling rate, stored digitally, and output through a digital-to-analog interface (TDT DD1 module). Tones were then lowpass filtered at 8.5 kHz (TDT FT5 module) and attenuated (TDT PA4 module). Noise for the masked thresholds (Experiment 2) was generated with a waveform generator (TDT WG1 module) and bandpassed filtered between 200 to 8500 Hz using a Krohn-Hite 3550 filter and the TDT FT5 module. Noise was then flattened to approximately equal intensity ( $\pm 5$  dB) across the spectrum using a programmable filter (TDT PF1 module) and attenuated (TDT PA4 module). Tones and masking noise (if present) were mixed (TDT SM3 module) and passed through a headphone buffer (TDT HB6 module) to allow monitoring by the experimenter, and they were then sent to the speaker in the chamber. Stimulus intensity was calibrated with a Larson Davis System 824 sound level meter (Larson Davis, Provo, UT) with a 0.5-in. microphone mounted in the approximate position of the perched bird's head.

**Procedure.** Birds were trained by a standard operant autoshaping program to peck at the observation key until a tone was presented. A peck on the report key within 2.4 s of tone presentation resulted in 3.0 s of access to a food reward of husked millet seed. A failure to peck the report key within 2.4 s of stimulus presentation was recorded as a miss and started a new trial. Thirty percent of trials were sham trials, in which no target was presented. If a bird pecked the report key during a sham trial or at any other time other than during a target presentation, the lights in the chamber were extinguished for 5–10 s. Experiments 1 and 2 were detection tasks in which birds were rewarded for detecting the presence of tonal stimuli. Experiments 3 and 4 were discrimination tasks in which a repeating background tone was presented during the observation phase and birds were rewarded for pecking the report key within 2.4 s of the presentation of a target tone.

Stimuli were presented following the method of constant stimuli (Dooling & Okanoya, 1995); see below for details of the stimuli used in each experiment. Sessions with greater than 20% false-alarm rates were discarded; false-alarm rates were usually below 10%. Birds were tested until thresholds stabilized (400–600 trials), and final thresholds were calculated for the last 200 trials. In Experiments 1 and 2, thresholds were defined as the SPL at which the stimulus was detected 50% of the time. For the other two experiments, thresholds were defined as either the frequency difference (Experiment 3) or amplitude difference (Experiment 4) correctly detected 50% of the time.

### Experiment 1: Absolute Auditory Thresholds

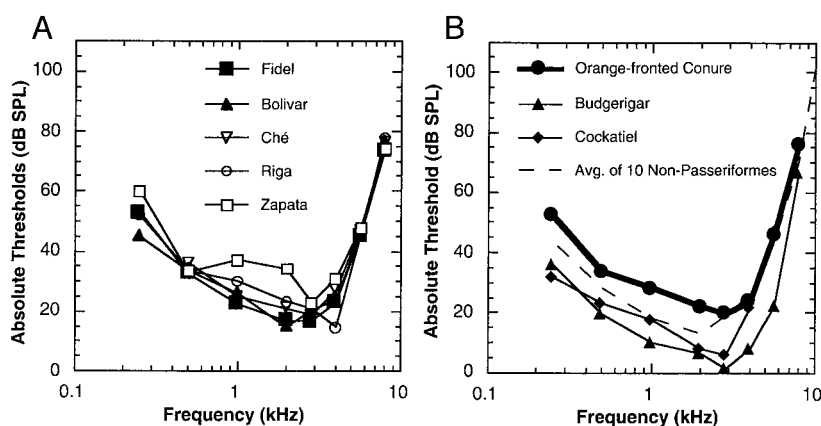
**Method.** We measured absolute auditory thresholds for 5 birds. We tested absolute sensitivity in the quiet at eight frequencies: 0.25, 0.5, 1.0, 2.0, 2.86, 4.0, 5.7, and 8.0 kHz with the exception of one bird who was not tested at 0.25 kHz. Tones were 200 ms long with a 5 ms linear rise–fall time and were generated at a sampling rate of 20.0 kHz. Step sizes were 10 dB for all frequencies except 8.0 kHz, for which we used 5 dB steps. Some birds were retested at selected frequencies in 5 dB steps; in these cases, we took the best threshold as the final threshold value.

**Results and discussion.** Audiograms for the individual orange-fronted conures are shown in Figure 3A, and the average audiogram for the 5 birds is shown in Figure 3B. All individuals showed a region of best hearing between 2.0 and 4.0 kHz. For frequencies descending below 2.0 kHz, threshold levels increased at a rate of 10 dB per octave, whereas above it thresholds increased at a rate of 50 dB per octave. This range of peak sensitivities corresponds fairly closely with the range of peak energy (2.0–5.0 kHz) in the averaged spectra for vocalizations as shown in Figure 2.

The average audiogram for the orange-fronted conure is similar in shape to those previously obtained for two other small parrot species, the budgerigar (Dooling, 1986) and the cockatiel (Okanoya & Dooling, 1987), with best thresholds for all three species recorded at 2.86 kHz (see Figure 3B). Thresholds for the orange-fronted conure are higher than those for the budgerigar throughout the range tested, with the difference ranging from 9 to 24 dB. Thresholds for the orange-fronted conure are also higher than those for the cockatiel between 0.25 and 2.86 kHz, with the difference ranging from 10 to 20 dB, but are equivalent at higher frequencies. Audiograms for all three parrot species are similar in shape and overall sensitivity to an average audiogram for 10 bird species not considered to be auditory specialists (i.e., not belonging to the orders Passeriformes or Strigiformes; Dooling et al., 2000).

### Experiment 2: Masked Auditory Thresholds

**Method.** We measured masked auditory thresholds for 3 birds in a manner similar to that used to measure absolute thresholds. In this experiment, white noise, bandpassed and flattened between 0.2 and 8.5 kHz, was



**Figure 3.** Absolute thresholds: Individual audiograms for 5 orange-fronted conures (A) and average audiogram for the orange-fronted conure (present study) plotted with audiograms for the budgerigar, the cockatiel, and an average (Avg.) audiogram reported by Dooling et al. (2000) for 10 species of avian auditory generalists (B). SPL = sound pressure level.

presented at an overall level of 60 dB SPL (measured with the Fast setting and A weighting on the sound level meter). We measured masked thresholds at six frequencies: 0.5, 1.0, 2.0, 2.86, 4.0, and 5.7 kHz. Tones were 200 ms long with a 5 ms linear rise–fall time and were generated at a sampling rate of 20.0 kHz. Step sizes were 10 dB for all frequencies. Some birds were retested at selected frequencies in 5 dB steps; in these cases, we took the best threshold as the final threshold value. We also measured masked thresholds for 2 birds at 2.86 kHz at three different overall noise levels: 50, 60, and 70 dB SPL. Critical ratios were determined by calculating the spectrum level (per cycle energy distribution) of noise in the octave band containing a given test frequency and subtracting it from the masked absolute threshold at that frequency.

**Results and discussion.** Critical ratio functions for individual orange-fronted conures are shown in Figure 4A, and the average function for the three birds is shown in Figure 4B. Critical ratios were relatively constant from 0.5 to 4.0 kHz then rose sharply above 4.0 kHz.

As shown in Figure 4B, the critical ratio function of the orange-fronted conure is similar to that previously found in the budgerigar and different from the typical pattern of an increase of 3 dB per octave (Dooling et al., 2000). Both parrot species are most sensitive to masked tones in the frequency range of the greatest spectral energy of their vocalizations.

As has been found in other studies (Farabaugh, Dent, & Dooling, 1998; Okanoya & Dooling, 1987), critical ratios were constant across a 20 dB change in the level of masking noise: average critical ratio at 2.86 kHz for a 50 dB SPL noise = 22.6, for a 60 dB SPL noise = 22.6, and for a 70 dB SPL noise = 22.8.

### Experiment 3: Frequency Difference Limens

**Method.** We measured FDLs in our subjects by measuring their ability to discriminate between a repeating background tone of a given frequency and alternating target tones of higher frequencies. We tested frequency discrimination abilities at six frequencies: 0.5, 1.0, 2.0, 2.86, 4.0, and 5.7 kHz. Tones were 200 ms long with a 10 ms linear rise–fall time and were generated at a sampling rate of 40.0 kHz. Target stimuli were presented in 10 Hz steps ascending from the background tone for all frequencies except 5.7 kHz, for which we used 50 Hz steps.

**Results and discussion.** FDLs ranged between 10 and 20 Hz for tones between 0.5 and 4.0 kHz then rose sharply to over 100 Hz

at 5.7 kHz (see Table 1). The average FDL function for the orange-fronted conure (see Figure 5) is similar in both shape and overall sensitivity to those for the budgerigar and an average curve for seven bird species (Dooling et al., 2000). As with the audiogram and the critical ratio function, orange-fronted conures have the lowest FDLs in the region corresponding to the greatest concentration of spectral energy in their vocalizations.

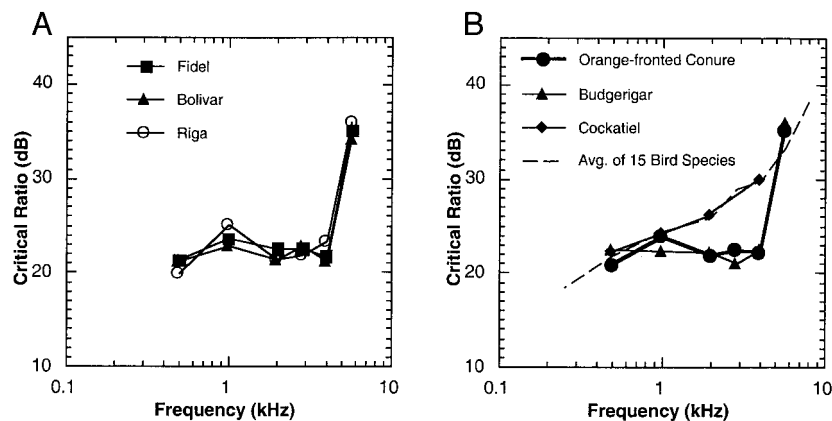
### Experiment 4: Intensity Difference Limens

**Method.** We measured IDLs in our subjects by measuring their ability to detect a difference between a repeating background tone of a given SPL and alternating target tones of a higher SPL. Intensity discrimination was measured at five frequencies: 1.0, 2.0, 2.86, 4.0, and 5.7 kHz. Tones were 200 ms long with a 10 ms linear rise–fall time and were generated at a sampling rate of 40.0 kHz. Target stimuli were presented in 2 dB steps ascending from the background tone presented at 70 dB SPL.

**Results and discussion.** IDLs for all frequencies were between 3 and 6 dB at 70 dB SPL (see Table 1). As shown in Figure 6, the average IDL for orange-fronted conures was 1–2 dB higher at a given frequency than an average IDL for three other bird species tested in a similar manner at 50 dB SPL (Hienz, Sinnott, & Sachs, 1980) and about 1 dB higher than the budgerigar tested at 2.86 kHz at 70 dB SPL (Dooling & Saunders, 1975a). These results are similar to other findings (Dooling & Searcy, 1979, 1981; Okanoya & Dooling, 1985), which taken together suggest that birds, in general, are not particularly sensitive to differences in intensity (Dooling et al., 2000).

## General Discussion

There are two main findings from our study of auditory sensitivity in the orange-fronted conure. The first is that the basic auditory abilities of this species are similar to those found in a wide range of avian auditory generalists, with a narrow region of best hearing between 2.0 and 4.0 kHz. The second is that there is generally a close correspondence in this species between the spectral region of greatest auditory sensitivity and the concentration of spectral energy in their vocalizations centered around 3.0 kHz.



**Figure 4.** Masked thresholds: Individual critical ratio functions for 3 orange-fronted conures (A) and average critical ratio function for the orange-fronted conure (present study) plotted with critical ratio functions for the budgerigar, the cockatiel, and an average (Avg.) function for 15 species of birds (B) reported by Dooling et al. (2000).

Table 1  
*Frequency Difference Limens (FDLs) and Intensity Difference Limens (IDLs) for Individual Orange-Fronted Conures*

Frequency (kHz)	FDLs (Hz)				IDLs (dB)			
	Fidel	Bolivar	M	SE	Fidel	Bolivar	M	SE
0.50	12.5	8.3	10.4	2.1				
1.00	14.6	17.5	16.0	1.4	4.3	6.0	5.1	1.2
2.00	12.5	15.4	14.0	1.4	4.4	4.0	4.2	0.3
2.86	16.2	20.0	18.1	1.9	3.8	5.2	4.5	1.0
4.00	18.0	16.7	17.3	0.6	4.2	3.6	3.9	0.5
5.70	125.0	145.4	135.2	10.2	2.8	5.0	3.9	1.5

We found that the functions for absolute thresholds, FDLs, and IDLs were all similar in overall sensitivity and general shape to those previously found in other small parrots and in a range of birds from other orders. These findings lend further support to the established view that basic hearing capabilities (and the auditory structures that give rise to them) are evolutionarily conserved over a wide range of avian taxa (Dooling et al., 2000). Although there are some trends across the group, such as better low-frequency hearing in larger birds and in nocturnal predators that hunt by auditory cues (e.g., Strigiformes), in general most birds have similar absolute auditory sensitivities (Dooling et al., 2000).

Although absolute auditory sensitivity may be fairly constant across birds, the ability to detect signals in the presence of masking noise appears to be less evolutionarily conserved. We found that orange-fronted conures exhibit an unusual critical ratio function similar to that previously found in the budgerigar. Both species show an area of decreased signal-to-noise ratio at thresholds between 2.0 and 4.0 kHz when compared with the typical avian function, which shows a monotonic decrease in sensitivity of 3 dB per octave from 0.25 to 8.0 kHz. Intriguingly, the single cockatiel that has been tested to date exhibits the more typical avian critical ratio function. Cockatiels are more closely related to budgerigars

than either are to the orange-fronted conure (Brown & Toft, 1999; Forshaw, 1989; Miyaki et al., 1998). The phylogenetic distribution of the enhanced sensitivity to masked tones suggests this character trait has either evolved more than once in the parrots or, as is perhaps more likely for a potentially complex trait, was present in the common ancestor of these parrots and was subsequently lost in the lineage leading to the cockatiel.

Similar variation appears in the Passeriformes, in which most species tested have a critical ratio function that increases about 3 dB per octave, whereas others exhibit functions that are markedly different (e.g., great tits, *Parus major*; red-winged blackbirds, *Agelaius phoeniceus*; and brown-headed cowbirds, *Molothrus ater*; Hienz & Sachs, 1987; Langemann, Gauger, & Klump, 1998). Although both the functional significance and the physiological underpinnings of these different critical ratio functions remain uncertain, these results suggest that the ability to detect signals in noise may be more evolutionarily labile than some other avian auditory capabilities. Noise from both biotic and abiotic sources is ubiquitous in nature, and the ability of the auditory system to detect and discriminate signals within the context of this masking noise is likely a critical factor in intraspecific communication (Ryan & Brenowitz, 1985; Wiley & Richards, 1978). Thus the characteristics of noise in the habitat of a given species as well as the acoustic characteristics of its communication signals may be

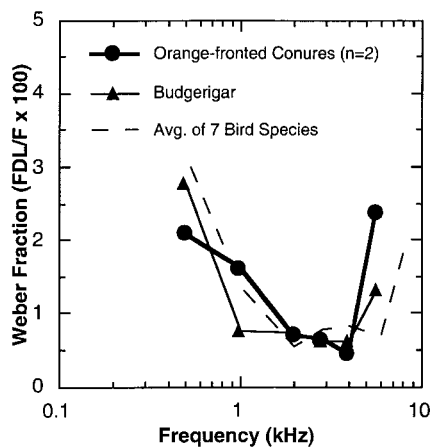


Figure 5. Frequency difference limens (FDLs) for the orange-fronted conure plotted as Weber fractions ( $FDL/F \times 100$ ). Also plotted are the mean FDL function for the budgerigar and an average (Avg.) FDL function for seven species of birds reported by Dooling et al. (2000). F = frequency tested.

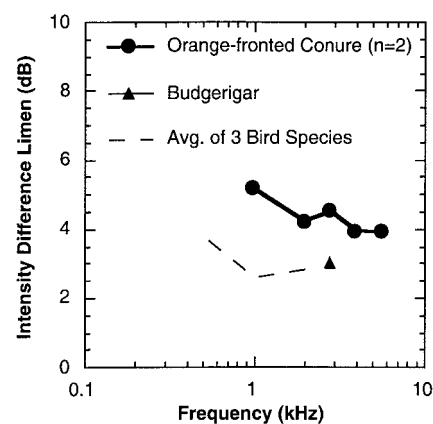


Figure 6. Intensity difference limens (IDLs) for the orange-fronted conure plotted with an average (Avg.) IDL function for three species of birds (Hienz et al., 1980) and a single IDL at 2.86 kHz for the budgerigar (Dooling & Saunders, 1975a).



important selective forces in the evolution of the auditory systems of different bird species.

The second main finding is that auditory and vocal production abilities appear closely matched in the orange-fronted conure. We found a close correspondence between the spectral range of greatest energy in the vocalizations in this species and the frequency range of greatest sensitivity for absolute thresholds, critical ratios, and FDLs. Both contact calls and the vocal repertoire as a whole had the greatest concentration of spectral energy around 3.0 kHz, with spectral energy concentrated between 2.0 and 5.0 kHz in contact calls and spread more widely between 1.0 and 7.0 kHz in a general sample of other vocalizations. Absolute thresholds, critical ratios, and FDLs all showed regions of greatest sensitivity between 2.0 and 4.0 kHz, with sensitivity falling off more quickly above 4.0 kHz than below 2.0 kHz. This region has been hypothesized to be a spectral window in an acoustic environment determined both by frequency-dependent attenuation and by high levels of ambient noise produced by wind (below 1.0–2.0 kHz) and insects (above 4.0 kHz; Klump, 1996; Ryan & Brenowitz, 1985; Wiley & Richards, 1978). Given that this spectral region probably provides the optimal signal-to-noise ratio for the vocalizations of many bird species, it is not surprising that many species, including the orange-fronted conure, produce vocalizations with energy concentrated in this region and that their auditory systems are most sensitive in this range.

One exception to this pattern of greatest sensitivity in the spectral range of vocalizations is in the discrimination of intensity differences. Given that most of the spectral energy in the contact calls of the orange-fronted conure is concentrated between 2.0 and 5.0 kHz, we might have expected IDLs to be smallest in that range. Instead, IDLs in the orange-fronted conure were generally high (around 4 dB) for all frequencies tested; similar results have been found in other birds (Dooling & Saunders, 1975a; Hienz et al., 1980). It is perhaps not surprising that intensity discrimination abilities do not correspond closely with vocal spectral characteristics given that intensity differences in acoustic signals are generally unreliable cues for communication in the wild. The intensity of a signal may vary greatly depending on a range of ecological factors such as distance from the source, ambient noise, and clutter in the environment or on the physiological state of a signaler (Wiley & Richards, 1978). Both types of factors may render intensity less suitable for encoding information than other acoustic features such as frequency or duration (Dooling et al., 2000; Wiley & Richards, 1978).

Our measures of hearing abilities in the orange-fronted conure are consistent with the idea that some auditory sensitivities in birds evolve to match the spectral characteristics of their vocalizations. It is important to note, however, that the evolutionary conservation of both vocal characteristics and many auditory sensitivities across birds makes it difficult to distinguish between ongoing coevolution of these traits and simple phylogenetic inertia (or possibly physiological constraints). The repeated evolution of unusual critical ratios in both parrots and passerines could provide one avenue for testing these alternatives through comparative studies of closely related species in different acoustic environments and with different vocal characteristics. Such studies will further our understanding of the relationship between signal production and reception in avian communication.

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