ASHMOLE, N. P. 1961. The biology of certain terns. D. Phil. thesis, Oxford Univ.

BENNETT, P. M. 1986. Comparative studies of morphology, life history and ecology among birds. Ph.D. thesis, Univ. Sussex.

BLACKBURN, T. M. 1990. A comparative examination of animal life history evolution. D. Phil. thesis, Univ. Oxford.

———. 1991. The interspecific relationship between clutch size and egg size in wildfowl. Auk 108: 209-211.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Am. Nat. 125: 1-15.

HARVEY, P. H. 1982. On rethinking allometry. J. Theor. Biol. 95: 37-41.

———, & M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford, Oxford Univ. Press.

———, ———, & J. A. REES. 1991. Mammalian metabolism and life histories. Am. Nat. In press.

HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210: 1148-1150.

HOWARD, R., & A. MOORE. 1984. A complete checklist of the birds of the world. London, Macmillan.

KLEIBER, M. 1962. The fire of life. New York, John Wiley & Sons.

KLOMP, H. 1970. The determination of clutch size in birds. A review. Ardea 58: 1-124.

LACK, D. 1967. The significance of clutch size in waterfowl. Wildfowl 19: 67-69.

———. 1968. Ecological adaptations for breeding in birds. London, Methuen & Co.

NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

PAGEL, M. D., & P. H. HARVEY. 1988. Recent developments in the analysis of comparative data. Q. Rev. Biol. 63: 413-440.

———, & ———. 1989. Comparative methods for examining adaptation depend on evolutionary models. Folia Primatol. 53: 203-220.

PARTRIDGE, L. 1990. Lifetime reproductive success and life history evolution. Pp. 421-440 *in* Lifetime reproduction in birds (I. Newton, Ed.). London, Academic Press.

READ, A. F., & P. H. HARVEY. 1989. Life history differences among the eutherian radiations. J. Zool. London 219: 329-353.

RICKLEFS, R. E. 1977. A note on the evolution of clutch size in altricial birds. Pp. 193-214 *in* Evolutionary ecology (B. Stonehouse and C. M. Perrins, Eds.). London, MacMillan & Co.

———. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38-49.

ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk 105: 161-176.

———. 1991. Response to T. M. Blackburn. Auk 108: 211-213.

SAETHER, B-E. 1988. Pattern of covariation between life-history traits of European birds. Nature 331: 616-617.

SIBLEY, C. G., J. E. AHLQUIST, & B. L. MONROE JR. 1988. A classification of living birds of the world based on DNA-DNA hybridization studies. Auk 105: 409-423.

SIBLY, R. M., & P. CALOW. 1986. Physiological ecology of animals: an evolutionary approach. Oxford, Blackwell Sci. Publ.

STEARNS, S. C. 1989. Trade-offs in life history evolution. Funct. Ecol. 3: 259-268.

SMITH, C. C., & S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. Am. Nat. 108: 499-506.

VAN NOORDWIJK, A. J., & G. DE JONG. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128: 137-142.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton, New Jersey, Princeton Univ. Press.

Received 20 April 1990, accepted 27 May 1991.

Use of the Relative Frequency of Notes by Veeries in Song Recognition and Production

DANIEL M. WEARY,[1] RONALD G. WEISMAN,[2] ROBERT E. LEMON,[1]
TINA CHIN,[2] AND JOHANNE MONGRAIN[1]
[1]*Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, Quebec H3A 1B1, Canada, and*
[2]*Department of Psychology, Queen's University, Kingston, Ontario K7L 3N6, Canada*

The relative frequency of notes is an important feature in the perception of tonal sequences by humans (Deutsch 1982). That is, humans can recognize a tune despite shifts in frequency (for example, a change of octave) so long as the ratio between the frequencies of the notes is preserved. In the music perception literature, the processing of frequency relationships has been subdivided into two categories: frequency contour processing, which uses the direction but not the amount of change, and frequency ratio processing, which uses both the direction and amount of change (Deutsch 1982). In principle, hu-

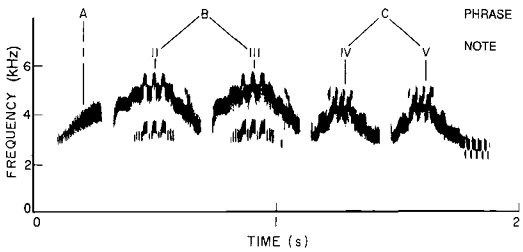

Fig. 1. A wide band sonogram of a typical Veery song illustrating the three phrases (A, B, & C) and five notes (I–V).

mans could use the linear difference between frequencies to recognize a tune, but the overwhelming evidence is that the log difference (the frequency ratio) is the key feature.

It is not known if other animals recognize sounds in a similar way. For example, perhaps birds can recognize conspecific song even when it has been shifted in frequency, so long as the relative frequency of the components has been maintained. Until very recently, the contribution of relative frequency to song recognition was unexplored. Now, research on two species of birds with simple, clearly whistled songs have indicated that the frequency relationship between notes is an important feature in recognition (Weisman and Ratcliffe 1989, Hurly et al. 1990). Black-capped Chickadees (*Parus atricapillus*) and White-throated Sparrows (*Zonotrichia albicollis*) showed stronger territorial response to songs with a normal frequency ratio than to songs with abnormal ratios.

Detailed studies of how White-throated Sparrows and Black-capped Chickadees sing their songs have also pointed towards a strong effect of the relative frequency of song notes, and specifically the frequency ratio. In both species, the ratio was highly consistent among individuals over a range of frequency values (Hurly et al. 1991, Weisman et al. 1990). In other words, regardless of the specific frequency at which these birds sing one note, the other is sung at a constant species-typical ratio of it.

These results for the simple tonal songs of the Black-capped Chickadee and White-throated Sparrow are intriguing. Operant discrimination experiments on a bird that produces a more complex song (the European Starling, *Sturnus vulgaris*) provide evidence that perception of pitch contour is constrained by absolute frequency perception; but there is no evidence for the perception of frequency ratio (Hulse and Cynx 1985, 1986; Page et al. 1989). Veeries (*Catharus fuscescens*) also sing complex songs with many frequency and amplitude changes within and between song notes (Fig. 1). Field playback experiments (MacNally et al. 1985, Weary et al. 1986) suggest that a major change in frequency between the two main phrases in Veery song is important for song recognition. To determine the contribution of relative frequency to this change, we analyzed song production in a large sample of songs recorded in the wild, and then we performed a playback experiment to test song recognition.

Songs of 61 adult male Veeries were recorded from various locations in North America. Weary recorded 11 birds from St. Andrews, New Brunswick, and 10 birds from Mont St. Hilaire, Quebec. Additional samples were acquired from the Cornell University Library of Natural Sounds (19 birds) and the Ohio State University's Borror Laboratory of Bioacoustics (21 birds). The Cornell and Borror samples were from a variety of geographic locations, divided for our analyses into eastern (25 birds) and western (15 birds) North America. From each bird, three consecutive high-quality recordings were analyzed, and mean values were recorded.

The song of the Veery consists of three phrases: an introductory note (A) about 10 dB quieter than the rest of the song, a pair of high frequency notes (B), and a pair of lower frequency notes (C) (Fig. 1). As the first phrase (A) does not appear to be important in song recognition (MacNally et al. 1985), we shall ignore it in this study. We measured the frequency of greatest energy (i.e. peak frequency on the spectrogram) for each note. We chose this measure of frequency, as we found it the most repeatable. Throughout this communication we use the term *frequency* to refer to this specific measure. We analyzed statistically the frequency relationship between the last note in phrase B and the first note in phrase C, as well as the relationship between the notes within each of the two phrases.

To measure frequency, we used the spectrographic display generated by MacSpeech Lab 2.0 software on a Macintosh computer. Songs were filtered (10.5 kHz low pass) and then digitized at a sampling rate of 22 kHz using a 12-bit D/A converter (MacADIOS 411) with a dynamic range of 72 dB. Spectrograms were generated with a 1,024 point FFT. The frequency resolution of this system was approximately 20 Hz.

The Veeries sang the pairs of notes within each phrase with a high degree of similarity. The two notes of phrase B had mean frequencies of 4,776 Hz (note II) and 4,774 Hz (note III) (paired t-test: $t = 0.50$, df $= 60$, $P = 0.618$) and were highly correlated across subjects (Pearson correlation coefficient $r = 0.996$). Similarly, the notes of phrase C had mean frequencies of 3,749 Hz (note IV) and 3,751 Hz (note V) ($t = 0.64$, df $= 60$, $P = 0.524$) and were also correlated ($r = 0.997$). Thus notes within each phrase can be considered nearly identical, and we can use the relationship between the adjoining notes of the two phrases (notes III and IV) to characterize the relationship between the phrases.

The relationship between the frequency of these notes was strong (Fig. 2). The frequency at which birds sang note IV (phrase C) was consistently lower than that of note III (phrase B) ($t = 63.00$, df $= 60$, $P = 0.0001$), but the two were highly correlated ($r =$

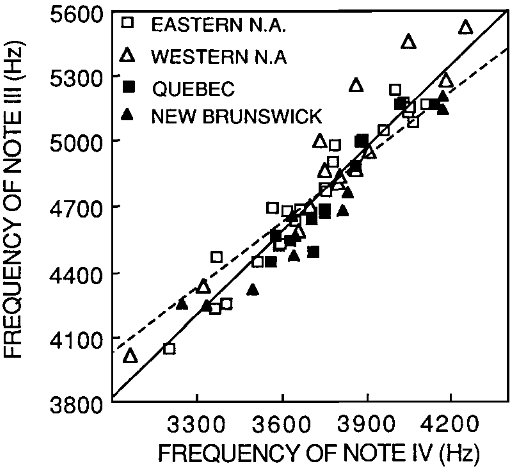

Fig. 2. A scatter plot of the relationship between the frequency of note III (phrase B) and note IV (phrase C). Two theoretical lines are shown. The continuous line represents the equation Note III = 1.273 (Note IV) and the dashed lines shows Note III = (Note IV) − 1,024. Birds from the four different regions are illustrated with different symbols, but there were no consistent differences between regions for either of the notes alone or the ratio of the notes (all $F_{3,57} <$ 1.25, all $P > 0.3$).

0.945, df = 59, $P = 0.0001$). These results demonstrate a precise relationship between the frequencies of the two phrases. There are two possible mechanisms by which the birds may be achieving this relationship. As the two sets of frequencies are linearly related (the addition of quadratic and cubic functions provide negligible improvements in fit) the relationship can be characterized theoretically from the general linear equation $y = ax + b$, or in the current example Phrase B = a(Phrase C) + b. To test if the Veeries' production rule is to produce a consistent frequency difference, we fitted an equation with the "b" term equal to the mean difference across our subjects (1,024 Hz) and the "a" term equal to one. Similarly, we tested if the production rule was to produce a consistent frequency ratio by fitting an equation with the "b" term equal to zero and the "a" term equal to the mean ratio (1.273). Although both lines appear to provide a good fit to the observed values (Fig. 2), we performed goodness-of-fit tests to determine which provided the greater explanatory value (the better the fit, the smaller the Chi-square value). The "ratio" model provided a better fit ($\chi^2 = 153.1$) to our data than did the "difference" model ($\chi^2 = 201.3$).

The above analyses led us to suggest that relative frequency is an important feature governing how Veeries sing. To determine if this feature was also important in song recognition, we performed a playback experiment. From our sample of recordings we constructed two versions of each of four test songs.

TABLE 1. Frequencies and frequency ratios of the test songs.

Test song	Phrase B (Hz)	Phrase C (Hz)	Frequency ratio
Version 1			
1B, 2C	5,371	4,246	1.26
3B, 4C	4,290	3,390	1.27
3B, 2C	4,290	4,246	1.01
1B, 4C	5,371	3,390	1.58
Version 2			
5B, 6C	5,126	4,105	1.25
7B, 8C	4,120	3,246	1.27
7B, 6C	4,120	4,105	1.00
5B, 8C	5,126	3,246	1.58

Songs were synthesized by combining phrases B and C from 8 different birds (1–8 *in* Table 1). A song with the normal frequency ratio (as determined from the above analyses) was formed by combining phrase B from Bird 1 with phrase C from Bird 2 (to form 1B, 2C *in* Table 1). Another song with normal ratio was formed in a similar way (3B, 4C), within the criterion that 2C and 3B were very similar in frequency. Thus, this second normal song was at a lower frequency than the first. We used the same phrases from these songs to form two new songs: one with virtually no change in frequency (3B, 2C) and one with double the normal ratio (1B, 4C). In an identical way, we used the songs from 4 new birds (Table 1) to form another version of each of these 4 test songs. All manipulations were performed digitally using SoundCap, SoundWave, and SoundEdit software. The formation of the test songs followed Hurly et al. (1990) and controls for the absolute frequency of the two phrases. Songs were recorded onto playback tapes at a rate that approximated natural rates of singing (8 songs/min).

Playback trials were performed between 0630 and 2135 Atlantic daylight savings time in June, 1989, on a population of territorial male Veeries near St. Andrews. Subjects were unbanded, but we reduced the probability of testing the same individual twice by moving a minimum of 500 m between trials. Our previous experimental work with known individuals from this area indicated that the largest territories were less than half this diameter.

We tested 28 subjects. Subjects were randomly assigned to one of the two versions of the test songs, and then to a counterbalanced order of the test songs. Each trial consisted of 9 periods. Trials began with a 2-min pre-stimulus silent period. The 4 test songs were then broadcast for 2 min each, separated by 4-min silent periods. Songs were played using a Marantz C-205 tape recorder, Toa amplifier, and Huber Cal 26 loudspeaker placed ca. 1.5 m off the ground. Maximum song intensity was standardized to 90 dB at 0.3 m from the loudspeaker.

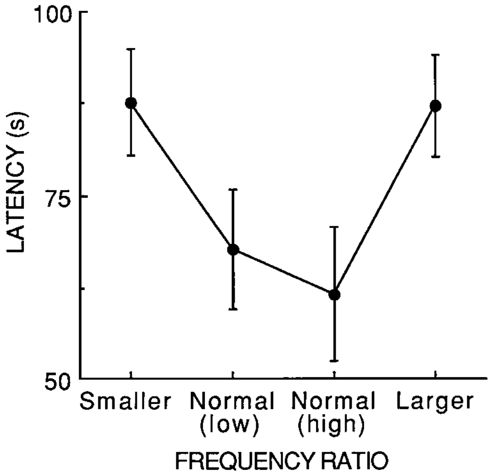

Fig. 3. Responses (mean ± SE) to the four types of test songs. There were two types of songs with normal frequency ratios: those with a relatively high starting frequency (Normal High) and those with a relatively low one (Normal Low). There were also two types of songs with altered ratios: those with a ratio of one (Smaller) and those with double the normal ratio (Larger). The response measure illustrated is latency to approach within 7 m of the speaker. The patterns were similar for the three other response measures.

We evaluated the response to playback during each 2-min stimulus period by four response measures: (1) the number of songs, (2) the number of movements, including hops and flights, (3) latency of approach to within 7 m of the loudspeaker, and (4) the minimum distance between the subject and the speaker. Measurements were recorded by three observers located at least 7 m from the loudspeaker. We conducted separate two-way (song version × frequency ratio) within-subject ANOVAs for each response measure.

Songs with the natural frequency ratio elicited a stronger territorial response than songs with either type of abnormal ratio (i.e. those songs with either no change in frequency or those with an abnormally large change in frequency) (Fig. 3). The Veeries sang more ($F = 5.67$; df = 1, 83; $P < 0.02$), made more movements ($F = 12.71$; df = 1, 83; $P < 0.001$), approached sooner ($F = 14.26$; df = 1, 83; $P < 0.001$), and approached closer ($F = 7.01$; df = 1, 83; $P < 0.01$) when songs with the natural ratio were played. We found no significant differences in response to the two versions of test songs for any of our measures, nor were the interactions between ratio and version statistically significant.

We conclude, from the analysis of natural songs and from the playback experiment, that Veeries use the relative frequency of notes to sing and recognize their songs. The data from our song recordings imply that Veeries sing songs with a constant frequency ratio over the range of absolute frequencies that naturally occur in their songs. The recognition experiment indicated that birds are sensitive to more than just the frequency contour, as the songs with the larger than normal frequency ratio elicited weaker responses. These playback results do not allow us to differentiate between the "difference" and "ratio" models. Indeed, the subjects may have been responding to any correlate of our independent variable, frequency ratio. However, our analyses of the song recordings demonstrated that Veeries produce a consistent frequency contour and that the precise relationship is best described by a consistent ratio of frequencies.

Our study indicates that relative frequency is important in song perception, but in no way rules out the importance of other song features. In fact, other experiments have shown that Veeries use a variety of song features to recognize songs (MacNally et al. 1985, Weary et al. 1986).

Our results are consistent with those from Black-capped Chickadees (Weisman and Ratcliffe 1989, Weisman et al. 1990) and White-throated Sparrows (Hurly et al. 1990), but not European Starlings (Hulse and Cynx 1985, 1986; Page et al. 1989). Veeries (which sing quite complex songs) seem to use relative frequency in song recognition and production. This argues against the possibility that the relative frequency of notes is important only to species that sing relatively simple songs. Our study, and those cited on Black-capped Chickadees and White-throated Sparrows, used territorial responses to natural songs to investigate perception. In contrast, the work on European Starlings employed an operant procedure and synthetic tones. We feel that it is unlikely that the difference between the studies relates to the use of a food-related task as opposed to a territorial one. Other tests of song perception in birds that have used both operant and playback techniques have indicated that these methods can produce similar results (see Weary 1989 and Weary et al. 1990, respectively). Also, a recent operant test on Black-capped Chickadees has shown a strong effect of relative frequency (Weary and Weisman 1991).

We thank Ann-Katrin Richter and Stephane Perreault for assistance in the field, Ingrid Johnsrude for assistance in the lab, Laurene Ratcliffe for advice at various stages of this research, and Andy Horn, Vivian T. Anderson, and David S. Dobkin for their insightful comments on the manuscript. Financial support was provided by FCAR Quebec and NSERC Canada post-doctoral fellowships to Weary, and by NSERC Canada operating grants to Weisman and Lemon.

LITERATURE CITED

DEUTSCH, D. (Ed.) 1982. The psychology of music. New York, Academic Press.

HULSE, S. H., & J. CYNX. 1985. Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus, Moluthrus,* and *Sturnus*). J. Comp. Psychol. 99: 176–196.

———, & ———. 1986. Interval and contour in serial pitch perception by a songbird *Sturnus vulgaris.* J. Comp. Psychol. 100: 215–228.

HURLY, T. A., L. RATCLIFFE, & R. G. WEISMAN. 1990. Relative pitch recognition in White-throated Sparrows (*Zonotrichia albicollis*). Anim. Behav. 40: 176–181.

———, R. G. WEISMAN, L. RATCLIFFE, & I. JOHNSRUDE. 1991. Absolute and relative pitch production in the song of the White-throated Sparrow (*Zonotrichia albicollis*). Bioacoustics: In press.

MACNALLY, R. C., D. M. WEARY, R. E. LEMON, & L. LEFEBVRE. 1985. Species recognition by song in the Veery (*Catharus fuscescens*: Aves). Ethology 71: 125–139.

PAGE, S. C., S. H. HULSE, & J. CYNX. 1989. Relative pitch perception in the European starling (*Sturnus vulgaris*); further evidence for an elusive phenomenon. J. Exp. Psychol.: Anim. Behav. Proc. 15: 137–146.

WEARY, D. M. 1989. Categorical perception of bird song: how do Great Tits (*Parus major*) perceive temporal variation in their song? J. Comp. Psychol. 103: 320–325.

———, J. B. FALLS, & P. K. MCGREGOR. 1990. Song matching and the perception of song types in Great Tits. Behav. Ecol. 1: 43–47.

———, R. E. LEMON, & E. M. DATE. 1986. Acoustic features used in song discrimination by the Veery. Ethology 72: 199–203.

———, & R. G. WEISMAN. 1991. Operant discrimination of frequency and frequency ratio in the black-capped chickadee (*Parus atricapillus*). J. Comp. Psych. In press.

WEISMAN, R. G., & L. RATCLIFFE. 1989. Absolute and relative pitch processing in Black-capped Chickadees, *Parus atricapillus.* Anim. Behav. 38: 685–692.

———, ———, I. S. JOHNSRUDE, & T. A. HURLY. 1990. Absolute and relative pitch production in the song of the Black-capped Chickadee (*Parus atricapillus*). Condor 92: 118–124.

Received 5 November 1990, accepted 27 May 1991.