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The Active Space of Red-Winged Blackbird Song

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Summary. Active space[1], that distance from the source over which signal amplitude remains above the detection threshold of potential receivers, was determined for Red-winged Blackbird (*Agelaius phoeniceus*) song in an upland pasture near Ithaca, New York. Song amplitude, the rate of signal attenuation, the amplitude of ambient noise, and the sensitivity of redwings to song masked by noise determine active space and were measured in the field:

1. Maximum root-mean-square song amplitude at 1 m from a singing bird ranged from 88.5–93.5 dB SPL ($\bar{X} \pm \mathrm{SE} = 90.8 \pm 0.21$ dB SPL).

2. Close to the source, song attenuates at a rate which closely matches that predicted by spherical spreading (6 dB/doubling of distance) alone. At distances beyond about 30 m, however, excess attenuation becomes important (Fig. 4). The rate of attenuation varies with relative wind direction (Table 1).

3. Ambient noise level is relatively low in early morning, rises in late morning and afternoon as air turbulence increases, and then drops again in the evening as turbulence decreases (Table 2 and Appendix). Measured on a 4 kHz octave filter scale (center frequency = 4 kHz, octave pass-band = 2.83–5.66 kHz), noise during one day ranges from 15 dB SPL (at 06:00 h) to 36 dB SPL (at 11:00 h), more than a 10-fold variation in ambient sound pressure.

4. A 3 dB signal to noise ratio is sufficient for detection of song masked by noise in the field (Figs. 5 and 6). Also, redwings are able to detect differences in this ratio as small as 3 dB.

5. In the absence of wind, the maximum active space of redwing song is about 189 m for a signal SPL of 93.5 dB at 1 m. This distance varies with changes in ambient noise level during the day, and with relative wind direction.

Maximum measurements of active space correspond closely to the maximum distances across 2 individual upland redwing territories. This suggests that redwing song is adapted in its structure and amplitude at the source to communicate a male's presence throughout the extent of his neighbors' territories.

Introduction

One of the most fundamental aspects of any signal used in animal communication is its active space, that distance from the source over which its amplitude remains above the detection threshold of potential receivers. For an acoustic signal active space is determined by 4 factors: (1) Amplitude of the signal at the source; (2) The rate at which signal energy attenuates with transmission through the environment; (3) Amplitude of ambient noise in the environment; and (4) Masked auditory threshold of receivers to the signal when embedded in a background of noise (Marten and Marler 1977; Waser and Waser 1977; Henwood and Fabrick 1979).

Knowledge of the distance over which a sound signal effectively transmits information would seem to be important in understanding its adaptive function. Surprisingly, though, active space has never been experimentally determined for any acoustic signal. Marten and Marler (1977) attempted to estimate the effective broadcast distance of Canary (*Serinus canarius*) song on the basis of empirical measurements of song amplitude and of sound attenuation in a North American habitat. This estimate has been called into

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Abbreviations: B & K Brüel and Kjaer; *RMS* root-mean-square; *S/N* signal to noise ratio; *SPL* sound pressure level (re: 20 μPa)

[1] While the term 'space' implies a three dimensional volume, 'active space' is used in this report to indicate a linear measure of a signal's maximum communication distance in the same sense as it was first applied to bird song by Marten and Marler (1977). This linear distance can be regarded as the radius of an effective communication volume

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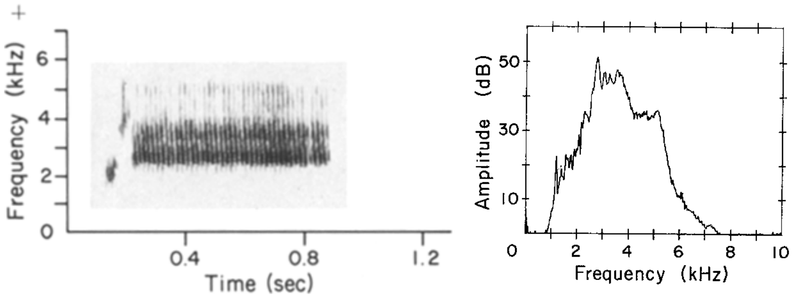

Fig. 1. Red-winged Blackbird song. Wide-band sound spectrogram on *left side*, power spectrum (relative amplitude vs frequency) on *right side*. This song was used in the masking playbacks

question, however, because of the frequency bandwidth over which they measured background noise level and their assumption that there would be no masking of song at the ambient noise level they present (P. Marler, personal communication). Henwood and Fabrick (1979) predicted 'broadcast area' with a mathematical model which considered only physical sources of attenuation; they too did not provide for masking of the signal. In the present study I measured each of the 4 factors described above for the song of the male Red-winged Blackbird (*Agelaius phoeniceus*) in order to obtain a more direct determination of active space.

Redwing song consists of a series of from 1–6 brief introductory components followed by a longer concluding trill, and has an average total duration of about 1 s (Fig. 1; also see Brenowitz 1982).

The trill is the most sustained and generally the most intense portion of this signal. Overall song frequency may range from about 1.0–6.0 kHz. Energy is seen in the trill from about 2.0–6.0 kHz, but is mostly concentrated in a band from about 2.5–4.0 kHz. This low frequency section of the trill is the part of the song that is transmitted over the greatest distance from a singing bird, and is shown by playback experiments to be both necessary and sufficient for species recognition (Brenowitz 1982). It contains adequate information for such recognition even after transmission over at least 100 m. Neither the introductory song components nor the higher frequency part of the trill (i.e. 4.0–6.0 kHz), both of which attenuate rapidly with distance from the source, are necessary or sufficient by themselves for species identification (Brenowitz 1981a, 1982).

As a signal such as redwing song attenuates with distance, it becomes increasingly susceptible to masking by environmental noise. For a signal of given spectral structure, the range of noise frequencies which will be effective in masking the signal is determined by the critical band function of the auditory system of the species in question. Critical bands have not yet been determined for redwings; the parakeet (*Melopsittacus undulatus*) is, in fact, the only avian species for which these data exist (Dooling and Saunders 1975; Saunders et al. 1978; Dooling 1980). Given the lack of information on blackbirds, a cautious extrapolation of the parakeet data is valid for several reasons: (1) The audibility curves of parakeets and redwings are very similar, with lowest absolute thresholds for both species occurring between 2–4 kHz, followed by a rapid rise in threshold above 4 kHz (63.7 dB/octave in parakeets, 70.0 dB/octave in redwings); (2) Both species show greatest frequency discrimination ability between 2–4 kHz. Critical bandwidth is commonly considered to be directly related to frequency selectivity; (3) In the songs of both species energy is concentrated at 2–4 kHz (Sachs et al. 1978; Saunders et al. 1978; Dooling 1980).

Playback experiments show that the part of the redwing song which conveys species identity is contained in the 2.5–4.0 kHz section of the trill (Brenowitz 1982). For the parakeet, the critical bandwidth at 2.0 kHz is equal to about 490 Hz, and at 4.0 kHz equals about 340 Hz (computed from 'Xind CB,' Table 1, Saunders et al. 1978). If these values are applied to redwings, they suggest that the essential 2.5–4.0 kHz trill band will be effectively masked only by noise between about 2.0 and 4.4 kHz.

The average power spectrum summed from hourly recordings of environmental noise from dawn to dusk on 1 day in the redwing breeding season is shown by Brenowitz (1982, Fig. 6). Between about 2.0 and 4.4 kHz the major biotic source of 'noise' arises from the vocalizations of various bird species. These are unlikely to significantly mask redwing song, however, given the discontinuous nature of most avian acoustic signals. Also, Cody and Brown (1969) showed that there tends to be temporal asynchrony in singing behavior of neighboring bird species. Furthermore, Wasserman (1977) found that, at least in White-throated Sparrows (*Zonotrichia albicollis*), individual birds avoid singing during the song of a conspecific. The other major biotic sound source in redwing habitats arises from the calls of various species of day-active Orthoptera. Starting in the latter part of the blackbird breeding season these insects

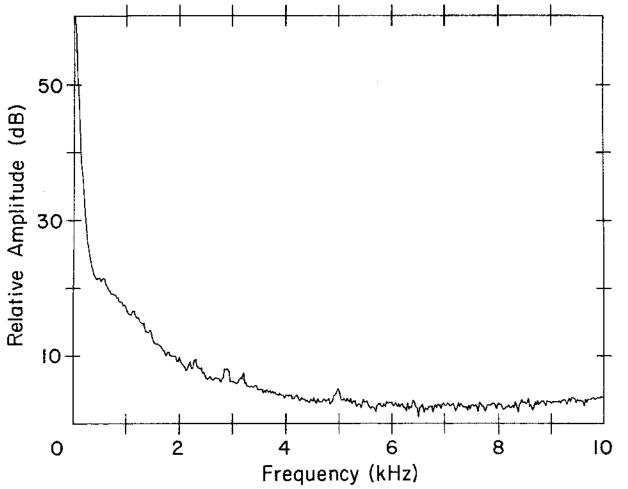

Fig. 2. Average power spectrum of wind-generated noise

provide a nearly-ubiquitous and continuous noise background. These signals contain energy only at high frequencies (≧8.3 kHz) outside of the effective blackbird song masking range of 2.0–4.4 kHz, however, and are thus unlikely to seriously interfere with conspecific song detection by redwings. The most likely remaining masking source is wind-generated noise. A recording of 'pure' wind noise over a 4-min period averaged continuously on a real-time fast Fourier analyzer has the power spectrum shown in Fig. 2 (see Brenowitz 1982 for methods).

Over the effective song-masking range of about 2.0–4.4 kHz the relative amplitude of this noise varies by ±3.3 dB. The experiments to determine the active space of redwing song described in this report were designed in accordance with this background information on avian masking functions and environmental noise structure.

Materials and Methods

Study Area. Redwings commonly breed in upland pasture areas near Ithaca, New York. Signal amplitude, song attenuation rate, and the amplitude of ambient noise were all measured in the same undisturbed open field in which the acoustic measurements presented in Brenowitz (1982) were made. This field consisted of tall grasses (≦0.75 m in height) with sparsely scattered shrubs and small trees typical of the early stages of secondary succession. In both years of the study (1980–1981), at least 15 male blackbirds defended territories in this field. Maximum distance across individual upland territories was on the order of 60–80 m (Howard 1977, and personal communication). Song was typically delivered from perches ≧1.5 m above the ground. Nests were built by females in the grass and shrubs. Playback experiments to determine the signal to noise ratio (S/N) for detection of masked song were conducted in this and other upland fields near Ithaca.

Amplitude Measurement. In masking studies the amplitude of broad-band noise is typically expressed in terms of spectrum level, which is defined as the sound pressure level falling at every single frequency within the noise bandwidth (Ehret 1977). This assumes, however, that such noise has equal amplitude at all frequencies. Inspection of Fig. 2 demonstrates that the power spectrum of wind noise, which constitutes the most likely masking source for redwing song, is by no means flat over the range of 0–10 kHz. Also, any measurement of ambient sound pressure level (SPL) on a linear unweighted scale will be strongly biased by the very intense sound energy at frequencies below about 100 Hz (see Appendix). This low frequency energy falls far below the predicted effective masking range of 2.0–4.4 kHz and outside the measured hearing range of redwings (Heinz et al. 1977). For these reasons, all sound pressure levels presented in this report were measured with a Brüel and Kjaer (B & K) type 1613 octave filter set adjusted to a 4 kHz center frequency and used in conjunction with a B & K type 2203 precision sound level meter.

The 4 kHz octave filter has an octave pass-band centered on 4 kHz and cut-off frequencies (3 dB attenuation) of 2.83 kHz and 5.66 kHz. Outside this octave pass-band the maximum attenuation slope is 45–50 dB/octave. The 2.5–4.0 kHz section of the trill, that contains the most energy in the redwing song and that is necessary and sufficient for species recognition, falls largely within the pass-band of this filter, as does the region of maximal auditory sensitivity in redwings. Readings of maximum root-mean-square (RMS) SPL of redwing song on the 4 kHz octave scale were within 0.5 dB of readings on a linear scale. Use of this filter was felt to be conservative since its relatively narrow pass-band would tend to underestimate the SPL of signals with energy outside this frequency band.

Signal Amplitude. To measure the amplitude at which song is produced, a Sennheiser MKH-415 T condenser microphone, mounted on a tripod at a height of about 1.5 m, was placed approximately 5 m from a small tree often used as a song perch by a male redwing. The male was called in to this perch by playback of conspecific song. Thirty-six songs given by this 1 bird were recorded at the same record level onto a Nagra IV-D recorder at 19 cm/s. Following this, a small (diaphragm diameter ca. 5.5 cm) Realistic 40–1277 Horn Tweeter was mounted on the same branch from which the recorded redwing sang, pointed in the same direction as was the bird's head. A recorded continuous 4 kHz tone was played over the tweeter at an amplitude of 89 dB SPL at 1 m, as measured with the B & K 2203 sound level meter (fast setting) on the linear unweighted scale. This tone was recorded for 4 min on the Nagra IV-D at the same record level used for the songs. The microphone was in the same position as for the recording of the songs. A 4 kHz test tone was used since this is approximately the center frequency of the trill.

In the laboratory the recorded signals were played through 2 Krohn-Hite 3550 filters connected in series, each set to a high-pass of 750 Hz to remove low-frequency background noise, into a Tektronix R564B storage oscilloscope. The amplitude of the 4 kHz calibration tone, measured as peak-to-peak voltage, was sampled at 20 arbitrarily determined intervals during the 4-min period[2]. For each recorded song the maximum peak-to-peak voltage was measured. Converting the ratio of the maximum song voltage to the average calibration tone voltage into decibels then allowed me to determine the maximum RMS SPL for each recorded song

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[2] When long duration tones of a single frequency are measured, standing waves and other interference phenomena may produce marked amplitude fluctuations. The low coefficient of variation (SD/X = 5.1%) for the 20 amplitude measurements of the 4 kHz calibration tone suggest, however, that the outdoor recording situation used was sufficiently free of interference effects to avoid this problem. The observed variation appeared to be due, rather, to short-term local fluctuations in air turbulence

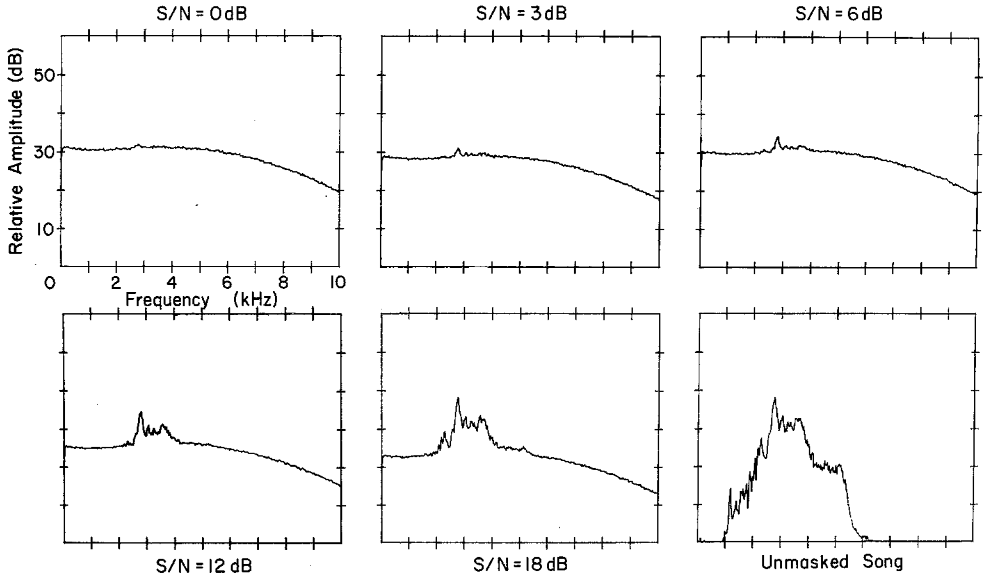

Fig. 3. Average power spectra of song masked by noise at various signal to noise (*S/N*) ratios, and of unmasked song. These stimuli were used in the masking playbacks

at a reference distance of 1 m from the source and on a linear unweighted scale. These are the values presented in Brenowitz (1981b). To convert these to SPL readings on the 4 kHz octave filter scale, I played a tape loop of one of the recorded songs from the Nagra IV-D to a Nagra DH loudspeaker mounted 1.5 m above the ground and read maximum RMS SPL at 1 m with the B & K sound level meter plus 4 kHz octave filter. This was done for each linear song SPL measured on the oscilloscope.

Rate of Signal Attenuation. The rate at which redwing song attenuates in energy with transmission over distance was measured in the main study field described above. A tape loop containing 1 blackbird song repeated at 3-s intervals was played from a Nagra IV-D recorder at 19 cm/s into an ADS-200 loudspeaker driven by a Nagra DH amplifier. This speaker was mounted on a platform 1.5 m above the ground and served as a reasonable approximation of a point source, given its small size (diaphragm diameter = 7.6 cm). Maximum RMS SPL of song playback was 89 dB at 1 m. Using the B & K 2203 sound level meter with the B & K 1613 filter set on the 4 kHz octave scale, the maximum RMS SPL of song was measured at about 5-m intervals over a total distance from the speaker of approximately 100 m. Ten readings were taken at each distance. These measurements were made within the first hour after dawn and were repeated on 12 days during and just after the breeding season. Data on temperature, relative humidity, and wind speed and direction for each sample period were supplied by the Atmospheric Sciences Department of Cornell University. These meteorological data were collected at a station located about 1.5 km from the main study field in similar open upland habitat. Temperature, humidity, and wind conditions were thus likely to be quite comparable at the two sites.

For each day, attenuation was computed by subtracting each SPL reading at each distance from the SPL reading at 1 m from the speaker. The mean attenuation value for each sampling distance was plotted against distance from the speaker and the equation of the line which best fit these data was calculated for each of the 12 days. Subsequently, these equations were used to predict the distance over which a given amount of attenuation would occur.

Amplitude of Ambient Noise. To measure the amplitude of ambient noise that could mask attenuated song I placed the B & K 2203 sound level meter (fast setting) with the B & K 1613 filter set on a mount 1.5 m above the ground in the main study field. Once each hour from dawn to dusk on 1 day early in the breeding season (3 May 1981) I took 20 readings at 3-s intervals of ambient noise on the 4 kHz octave scale and 20 readings on the linear unweighted scale. This day seemed to have meteorological conditions quite typical for that time of the breeding season.

Signal to Noise Ratio for Detection of Masked Song. It is difficult to measure absolute masked auditory thresholds behaviorally in a field setting. If a bird fails to respond to presentation of a low amplitude masked song, it is uncertain whether (1) this is due to an actual failure to detect the signal, or (2) the bird detects the signal but is not motivated to respond 'overtly' given the low amplitude (e.g. if the song is interpreted as being produced by a distant individual). Instead I attempted to determine a signal to noise ratio adequate for detection of masked song using signal amplitudes known from previous studies (e.g. Brenowitz 1982) to be sufficient to evoke responses. For sound pressure, $\mathrm{S/N} = 20 \log_{10}$ [Signal Prms/Noise Prms]. Knowing this ratio, for any given ambient noise level the song amplitude adequate for detection by blackbirds can then be determined.

I conducted playback experiments with 12 territorial male redwings to determine the signal to noise ratio for detection. From one channel of a Nagra IV-S stereo recorder I played at 9.5 cm/s continuous white noise recorded from a Grason-Stadler 1285 noise generator (10 kHz low-pass setting). Over the effective song masking range of 2.0–4.4 kHz, the noise amplitude varied by ±1 dB. Above about 6 kHz the noise amplitude fell (see Fig. 3), but this is outside the effective masking range. From the other channel the redwing song shown in Fig. 1 was played. These signals were passed to a Realistic 33–920 A battery-powered stereo-mixer that allowed the amplitude of the 2 channels to be controlled separately. The composite signal was played into a Nagra DH speaker placed in the central area of a male's territory. Strength of response to playbacks was quantified by the number of high intensity song spreads given by the bird during a 4-min test period. The song spread is a graded visual display that often accompanies song and that reflects corresponding gradation of aggressive arousal (Orians and Christman 1968; Peek 1972; Yasukawa 1981). Scoring only high intensity spreads is a conservative measure of response strength.

Experiments began with a 4-min silent baseline period. This was followed by 4-min of continuous noise alone. Five min later noise and song were played at the same maximum RMS SPL, as measured on the 4 kHz octave scale. Song was played at 15-s intervals for 3 min, followed by 1 min of post-playback observation. Noise was played continuously during the 4-min test period. In most cases the bird was within 10–15 m of the speaker at the playback onset. After another 5-min silent interval, the noise amplitude was decreased by 3 dB and presented with song in the same manner for 4 min. In successive 4-min playbacks, all separated by 5-min silent intervals, the noise amplitude was lowered to obtain the signal to noise ratios shown in Fig. 3. Noise level was not decreased in steps of less than 3 dB since there were short term fluctuations of ±0.5 dB inherent in the white noise used. At the end of this series, song was presented in the absence of noise. The sequence in which the different signal to noise ratios were presented was not randomized because an earlier study (Brenowitz 1981a) showed that strength of response to a signal of low stimulus value may be elevated due to arousal caused by prior exposure to a signal of high stimulus value. This could be important since in this experiment I considered the signal to noise ratio sufficient for detection as that ratio which evoked a first noticeable increase in response strength over the preliminary baseline level.

Data on number of songs, number and intensity of song spreads, latency to first song, and closeness of approach to the speaker were collected in each 4-min sample period. In a full playback series to 6 birds conducted from 9–16 June 1980, song amplitude was always set at 93.5 dB SPL on the 4 kHz octave scale at 1 m from the speaker. Noise level was successively lowered to a signal to noise ratio of 24 dB. Noise and song SPL's were calibrated both before and after each playback experiment. To determine whether the signal to noise ratio adequate for detection varied with signal amplitude, I repeated these playbacks with 6 other birds from 17–25 June 1980, but with song SPL reduced 6 dB to 87.5 dB at 1 m on the 4 kHz scale. This corresponds to a halving of amplitude. The same stimulus sequence as in the preceding playbacks was followed until a signal to noise ratio of 18 dB was reached.

Results

Signal Amplitude

The mean maximum RMS amplitude of 36 songs at 1 m on the 4 kHz octave scale was 90.8 dB SPL (SE = 0.21). Song SPL in this sample ranged from 88.5–93.5 dB.

Rate of Signal Attenuation

Results from 1 of the 12 measurements of song attenuation rate are shown in Fig. 4. Similar patterns were observed in the other samples.

The bars represent the mean ± 1 SE of 10 measurements of attenuation at each distance. The solid line is the attenuation that would be predicted from spherical spreading alone (6 dB/doubling of distance). Anything to the right of this line is excess attenuation (see Wiley and Richards 1978; Brenowitz 1982). As can be seen, attenuation measured near the speaker closely approximates the predicted losses; spherical spreading dominates at these short distances. But beyond about 30 m from the speaker, attenuation becomes greater than that predicted only from spherical spreading; excess attenuation becomes important at longer distances.

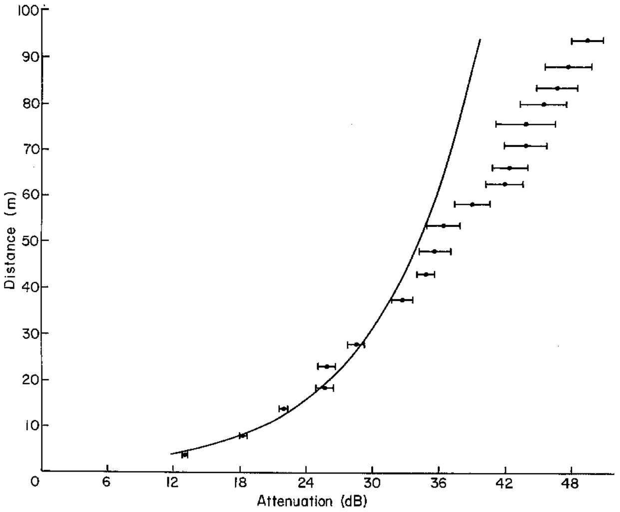

Fig. 4. Attenuation of song energy measured as a function of distance from the source. One redwing song was played repeatedly at 3-s intervals and the SPL was measured at about 5-m intervals on a 4 kHz octave filter scale. *Bars* indicate X ± 1 SE for 10 readings at each distance. *Solid line* indicates attenuation predicted by spherical spreading alone. (Distance from the source is presented as the dependent variable since this curve was used to predict the distance over which song SPL will attenuate by an amount which would define the boundaries of the active space.)

Several other observations emerge from inspection of Fig. 4. The variance in measured SPL and attenuation, as indicated by SE, increased with distance from the speaker (range = 0.07–0.52). Coefficients of variation (SD/X) for the data in Fig. 4 ranged from 0.25–5.79% and were also highly correlated with distance from the source ($r = 0.92$). (Coefficients of variation for the other trials showed the same trends and were comparably low in magnitude.) Near the speaker short-term amplitude fluctuations rarely exceeded ±1 dB. Further from the source, however, fluctuations in RMS SPL could equal or exceed ±3 dB over the 30-s sample period. Also, while over the entire distance range the pattern of attenuation was best described by an exponential equation, at distances beyond about 30 m the attenuation data best fit a linear regression. This results from the short-range dominance of spherical spreading, which is exponentially related to distance. Since song will attenuate to the low amplitude levels defining the boundaries of active space only at relatively long distances from

Table 1. Linear regression equations and associated meteorological data for measurements of signal attenuation rate on 3 different days. Attenuation rate was calculated as the inverse of the X-coefficient. For wind direction, + indicates receiver located downwind of source and – indicates receiver located upwind of source. * indicates $P<0.001$ (ANOVA)

Regression equation	r^2	Attenuation rate (dB/m)	Average wind speed (km/h) and direction	Average temperature (°C)	Relative humidity (%)
$X=-84.72+3.77X$*	0.98	0.265	+14.82	11.1	86
$Y=-66.69+3.39X$*	0.95	0.295	0	7.2	80
$Y=-33.13+2.28X$*	0.92	0.439	−7.61	8.9	92

Table 2. Ambient noise levels (X±SE, absolute minimum and absolute maximum) measured on a 4 kHz octave filter scale each hour from dawn to dusk on one day in the breeding season. For each ambient noise level the active spaces predicted using the 3 regression equations from Table 1 are shown

Time (h)	Ambient noise level (dB SPL)	Active space (m)		
		$Y=-84.72+3.77X$	$Y=-66.69+3.39X$	$Y=-33.13+2.28X$
05:20	21.4±0.36	175.9	167.6	124.7
06:00	19.7±0.55	182.2	173.2	128.5
07:00	20.3±0.61	179.9	171.2	127.1
08:00	18.8±0.36	185.5	176.3	130.5
09:00	20.2±0.40	180.4	171.6	127.4
10:00	20.9±0.64	177.7	169.2	125.8
11:00	26.2±0.96	157.8	151.3	113.7
12:00	21.8±0.51	174.5	166.4	123.8
13:00	24.7±0.87	163.4	156.4	117.1
14:00	23.6±0.73	167.6	160.1	119.6
15:00	24.8±0.48	163.0	156.0	116.9
16:00	22.6±0.81	171.1	163.3	121.8
17:00	22.7±0.75	171.0	163.2	121.7
18:00	19.2±0.43	184.2	175.0	129.7
19:00	23.8±0.78	166.8	159.4	119.2
20:00	18.8±0.44	185.4	176.2	130.5
20:20	24.7±0.65	163.4	156.4	117.1
Absolute minimum	15	200	189.3	139.3
Absolute maximum	36	120.8	118.1	91.3

the source, I felt the linear regression to be a better predictor of the distance at which this will occur. Thus for each of the 12 measurements of song attenuation rate I computed the linear regression equation that best fit readings of attenuation at and beyond 30 m.

Table 1 presents representative linear regression equations and associated meteorological data for 3 days. These (and the other 9) regressions are all significant at $P<0.001$ (ANOVA). The high coefficients of determination (r^2) indicate that nearly all of the observed variance in attenuation can be accounted for by distance from the speaker. Comparison of the 3 equations indicates that relative wind direction has an important effect upon the rate of attenuation. Placing the receiver downwind of the source reduces the rate of attenuation, and placing it upwind of the source increases the attenuation rate, compared to the rate seen in the absence of wind. Attenuation rates for the other 9 days fall within the range shown in Table 1. There was no simple correlation between rate of attenuation and either wind speed ($r=-0.096$), temperature ($r=0.047$), or relative humidity ($r=-0.083$).

Amplitude of Ambient Noise

The mean ambient noise level measured on the 4 kHz octave scale each hour from dawn to dusk on 1 day during the breeding season is shown in Table 2.

The noise level was relatively low in the early morning, rose in late morning and afternoon as air turbulence increased with heating of the ground (see Wiley and Richards 1978), and then dropped again in the evening as air turbulence decreased. The elevation in noise level at evening twilight (20:20 h) was due to a rapid onset of massive calling by frogs (Spring Peepers, *Hyla crucifer*). The absolute

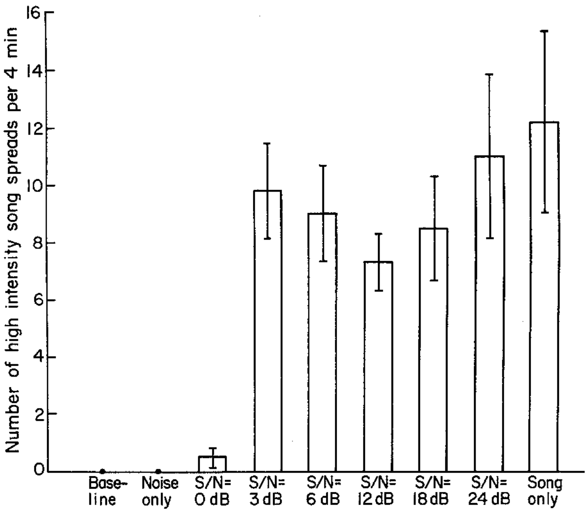

Fig. 5. Number of high intensity song spreads per 4-min test period (X ± 1 SE) given by Red-winged Blackbirds ($n=6$) in response to masking playbacks with song amplitude = 93.5 dB SPL at 1 m

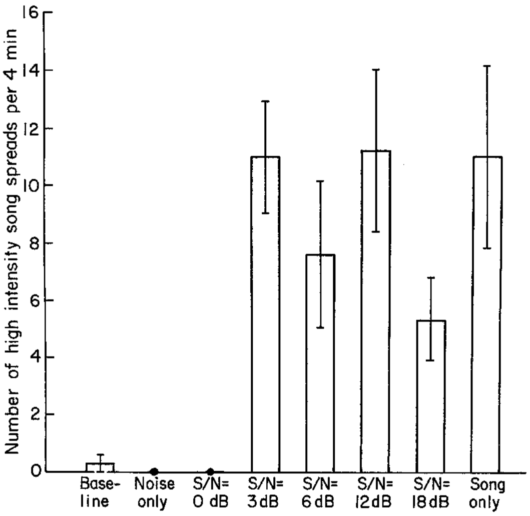

Fig. 6. Number of high intensity song spreads per 4-min test period (X ± 1 SE) given by redwings ($n=6$) in response to masking playbacks with song SPL = 87.5 dB at 1 m

minimum noise level measured on this day was 15 dB SPL (at 06:00 h), and the absolute maximum was 36 dB SPL (at 11:00 h). This 21 dB range corresponds to a more than 10-fold variation in ambient sound pressure during 1 day. Readings of ambient noise level on the linear unweighted scale are shown in the Appendix. The average power spectrum of environmental noise summed from hourly recordings is presented in Brenowitz (1982, Fig. 6).

Signal to Noise Ratio for Detection of Masked Song

Responses of 6 blackbirds to masking playbacks with song amplitude at 93.5 dB SPL at 1 m are shown in Fig. 5. No high intensity song spreads were seen during the silent baseline and noise-only periods. Two birds gave 2 high spreads and 1 bird gave 3 high spreads when song and noise were played at the same amplitude (S/N = 0 dB). There was a dramatic increase in the level of responsiveness, however, when noise level was lowered to a S/N ratio of 3 dB. All 6 birds gave strong responses at this ratio. (Control playbacks involving repeated presentation of the 0 dB S/N ratio signal did not show an increase in responsiveness.) The subsequent drop in mean number of high spreads to S/N = 12 dB seen in Fig. 5 does not reflect a lack of response. Rather, as the experiment proceeded through and beyond the S/N = 3 dB playback, males typically approached to within 5 m of the speaker and then seemed to listen intently to the playbacks and search in the surrounding grass for the apparent intruder while giving alarm calls as well as song. Though not giving as many songs with high spreads as earlier in the experiment, these birds were clearly giving responses oriented to the playback. As the experiment then continued, and the birds failed to locate an intruder, the number of high spreads seen during the 4-min periods increased again.

Figure 6 presents the responses of 6 birds to masking playbacks with song SPL = 87.5 dB at 1 m. One male gave 2 high spreads during the silent baseline period. No high spreads were given during the noise-only or S/N = 0 dB playbacks. When the S/N ratio was increased to 3 dB, however, there was a sharp increase in strength of response. This is the same pattern as seen in Fig. 5 for the song SPL = 93.5 dB playbacks.

These observations suggest that for male redwings to detect masked song in a field setting it is sufficient that song amplitude be 3 dB above the background noise amplitude, and that over the range tested this S/N ratio does not vary with signal SPL. It is worth noting, in addition, that redwings are apparently able to detect differences in signal to noise ratio as small as 3 dB (0 dB vs 3 dB). In Fig. 6 the decreases in mean number of high spreads in the 6 dB and 18 dB S/N playbacks can be explained as above for similar drops in Fig. 5.

Active Space

Active space was computed as the distance predicted from the linear regression equations over which song SPL attenuates from a maximum of 93.5 dB at 1 m to a level 3 dB above the ambient noise level. 93.5 dB is the maximum song amplitude measured on the 4 kHz octave scale and 3 dB is the signal to noise ratio for song detection obtained from the masking playbacks. Table 2 presents separate predicted active space values for the mean ambient noise levels measured each hour from dawn to dusk on 1 day in the breeding season, using the 3 linear regressions in Table 1. Thus Table 2 illustrates the variation in active space (1) with time of day as a function of ambient noise level and (2) at the same time on different days as a function of changes in rate of song attenuation due to different meteorological conditions.

Over the progress of a given day, the active space of song may vary by up to 30 m with changes in the mean ambient noise level. These daily variations are even more pronounced when one considers the absolute maximum and minimum noise levels. In the absence of wind, song would remain effective over a distance of about 189 m in the early morning when background noise level is at its lowest. As the ambient noise rises to its highest point in late morning, the effective distance of song would drop to about 118 m. This difference of over 70 m during 1 day can be compared to the maximum distance across an individual upland redwing territory of 60–80 m.

With a steady wind of 14.8 km/h blowing from the source in the direction of the receiver, the active space at the time of the lowest ambient noise level would be about 200 m. As the noise level rises to its maximum, active space of redwing song would fall to about 121 m, a total decrease of nearly 80 m.

Alternatively, with a wind speed of about 7.6 km/h and the receiver located upwind of the source, the maximum active space would be only approximately 139 m under the quietest conditions. With an increase in ambient noise to its greatest level, the active space drops to about 91 m. The total variation over this 1 day amounts to 48 m.

Comparison of predictions on the 3 days presented in Table 2 indicates that relative wind direction has a considerable effect upon the active space of song. For the lowest ambient noise level (15 dB), maximum active space with a receiver located upwind of the source may be as much as 60 m less than with the same receiver downwind of the sender.

Discussion

Signal Amplitude

Brackenbury (1979) measured maximum song amplitude in 17 European songbird species. The SPL values reported for redwing song in the present study fall within the range given for these 17 species (74–100 dB SPL at 1 m). Thus, while redwings are capable of producing song with considerable amplitude, they are not exceptional among oscine birds in their ability to do so.

Rate of Signal Attenuation

Over short distances from the source song attenuates at a rate predicted by spherical spreading alone, but excess attenuation due to such factors as absorption, refraction, and reflection of sound energy becomes important at distances beyond about 30 m. Dabelsteen (1981) found that the song of the European Blackbird (*Turdus merula*) also attenuates over short distances according to the predictions of inverse square attenuation. From studies of pure tone and white noise transmission, Marten and Marler (1977) reported the same trends over distance as found in the present study. As they observed, this trend can be explained by the fact that inverse square attenuation is proportional to the square of distance travelled by sound whereas excess attenuation tends to have more of a linear relationship to distance. This also explains why excess attenuation becomes consistently greater with increasing distance, as seen in Fig. 4.

The variance in measured SPL and attenuation increased with distance from the speaker. Richards and Wiley (1980) similarly found short-term fluctuations in amplitude that increased with increasing distance from the transmitter. They observed that the magnitude of such amplitude fluctuations was strongly dependent on wind speed near the ground and resultant turbulence.

The intensity of such fluctuations varies in correspondence with changes in atmospheric conditions over very short time periods. Furthermore, as distance from the source increases, the potential number of nonstationary heterogeneities (Wiley and Richards 1978), such as swaying vegetation or very local atmospheric turbulences, between the source and receiver increases. Each heterogeneity can introduce temporal fluctuations in signal strength and, to some extent at least, may be out of phase with others. As total distance from the transmitter increases, then, the potential overall magnitude of amplitude fluctuations, which at any one time represents the vector sum of contributions from the different sources, also increases.

The low coefficients of variation for measured attenuation (e.g. 0.25–5.79%) indicate that distances predicted from the regression equations and, consequently, active space estimates, will have a maximum possible error of about 6%. This corresponds to a maximum potential variation in active space of on the order of 12 m or less. Such small relative variation does not significantly influence the conclusions that can be drawn from this study.

Amplitude of Ambient Noise

Ambient noise level was relatively low in early morning, rose in late morning and afternoon, and then fell again in the evening. This pattern was associated with variation in atmospheric turbulence and wind over the day. Both turbulence and wind are greatest at midday when solar heat produces pronounced temperature gradients (see Ingard 1953; Wiley and Richards 1978; Richards and Wiley 1980). The movement of air past the ground, vegetation, and an animal's head generates ambient noise.

Waser and Waser (1977, Fig. 2C) measured ambient noise level on the relatively flat 'C' scale of a sound level meter near the ground of West African coastal forests in Cameroon. The noise levels they report are comparable in magnitude to those measured on the linear unweighted scale in the present study (Appendix). They also indicate that noise level was greatest at midday, and lower in early morning and evening. In addition they found a range in overall noise level over the progress of a day of approximately 20 dB, as I did in my measurements.

Signal to Noise Ratio for Detection of Masked Song

The masking experiments indicated that a signal to noise ratio of 3 dB was sufficient for detection of song embedded in a background of noise. The S/N ratio necessary for such detection apparently falls between 0–3 dB. Even if this ratio were as low as 0 dB, however, predictions of maximum active space would be increased by at most 17 m (ca. 8%). Thus estimates based on a S/N of 3 dB are conservative, and the major conclusions that can be drawn are not affected by where between 0–3 dB the necessary ratio does in fact lie.

Heinz et al. (1977) found that maximum behavioral auditory sensitivity in redwings occurred in the region of 2–4 kHz where thresholds in different individuals ranged from 4–20 dB SPL. The absolute minimum noise level on the 4 kHz octave scale measured in the present study was 15 dB SPL, which is higher than the absolute threshold for most birds to the frequency band of the song section necessary and sufficient for species recognition. Therefore, even if we assume that a 0 dB S/N ratio is adequate for masked song detection, it is likely that for most redwings the maximum distance over which song amplitude remains sufficient will be set by the ambient noise level rather than the absolute auditory threshold.

Redwings are able to detect a difference in S/N ratio as small as 3 dB. This corresponds to a sound pressure ratio of only 1.4:1.0. Interestingly, King et al. (1981) reported, in a different context, that Brown-headed Cowbirds (*Molothrus ater*) are also able to detect a change in S/N ratio of 3 dB.

Effect of Air Turbulence on Active Space

Comparison of active space predictions for the 3 days presented in Table 2 suggests that relative wind direction has an important effect upon the maximum effective distance of song. The atmosphere behaves as a fluid in continuous motion over the earth's surface. The velocity of air at the ground is zero due to friction but increases with height over the ground. The velocity of sound is the vector sum of the velocity of sound in air and the velocity of the air itself. Because air velocity increases with height, sound waves are refracted back towards the ground in the downwind direction and up away from the ground in the upwind direction. Upwind propagation, then, results in a shadow zone in which amplitude may be attenuated by as much as 30 dB. Amplitude reinforcement occurs in the downwind direction but the increases are generally much less in magnitude than the upwind attenuation. This last point probably explains the observation from Table 2 that the increase in maximum active space in the downwind trial relative to the windless trial is only 11 m, whereas the maximum active space decrease in the upwind trial relative to the windless trial is 50 m, despite the greater velocity of the downwind than of the upwind. Downwind reinforcement and upwind attenuation will result in an asymmetric sound field around the source in the presence of wind. Wind velocity in general tends to be greatest at midday (Ingard 1953; Wiley and Richards 1978; Hassall and Zaveri 1979; Henwood and Fabrick 1979; Richards and Wiley 1980).

The above discussion only considers the effect of a continuous, uniform wind. Winds tend to be gusty or turbulent, however, and such gustiness increases with wind velocity. Gustiness is minimal in early morning and evening, and is greatest at midday. Such turbulence can cause an average attenuation of sound energy of 4–6 dB/100 m, but this may go as high as 20 dB/100 m (Ingard 1953), and is largely the result of eddies of different sizes that travel along with the wind. Sound waves striking an eddy are all deviated in the same direction, regardless of which side of the axis they pass, depending only upon the eddy's direction of rotation. Deviations may be 2° or more in magnitude, and if a wave passes through several eddies its path may change considerably. This suggests that the directional reliability of a signal will decrease over distance from the source, and that this effect will be most pronounced at midday when turbulence is maximal.

The layer of air in which eddies occur may extend up to 500 m in altitude. Air turbulence, therefore, is likely to be an important factor in the evolution of acoustic signal structure and signalling behavior (see Wiley and Richards 1978; Richards and Wiley 1980). Since turbulence is greatest at midday, animals that use acoustic signals for long-range communication will benefit by concentrating their signalling behavior in early morning and/or evening. Redwings, in fact, sing most often at these times of day (Orians and Christman 1968; personal observation), as do many other animals.

My measurements of signal attenuation rate were made in early morning. Predictions of active space for each hour from dawn to dusk were based on these regressions. The preceding discussion of air turbulence, however, suggests that sound will not attenuate in the same way at midday as it does in early morning. This was confirmed by measurements of attenuation rate which I made in the afternoon. At this time of day there was no longer a consistent linear relationship between distance and attenuation. Instead I found unpredictable and often quite major changes in SPL with relatively minor changes in distance, in addition to considerable short-term fluctuations in amplitude at any one distance. It seems likely, therefore, that increased attenuation from turbulence will reduce active space in late morning and afternoon below the predicted values in Table 2, resulting in even greater ranges in effective distance over the progress of a day. Since both steady winds and turbulence become minimal in the evening, sound probably attenuates then at a similar rate as in the early morning and active spaces late in the day are thus likely to be closely approximated by values shown in Table 2.

Territory Size and Active Space

Smith (1979) found that when he temporarily devocalized territorial male redwings, the frequency and length of intrusions on their territories by their neighbors increased considerably. Some of these muted birds remained on their territories. Over time, the territories of these birds were reduced in area as neighboring males extended their song perches and therefore their territory boundaries increasingly further into the silenced males' former areas. When these muted males regained their ability to sing, they were successful in regaining territory boundaries that approached or exceeded their original size. These results suggest that during the breeding season song is important in maintaining territorial boundaries between neighbors, most likely by informing neighbors of a territory owner's continued presence. Such an adaptation could be of selective advantage to individuals by inhibiting territorial intrusions that might lead to energy-expensive chases or injury.

To be most effective at fulfilling such a function, the active space of song should be sufficient to include the full extent of neighbors' territories. As stated earlier, the maximum distance across individual upland redwing territories is about 60–80 m. From Table 2, the active space of redwing song in early morning and evening in the absence of wind is on the order of 160–170 m. These values indicate that at the times of day when blackbirds sing most often, song will travel completely across the singer's territory and remain effective throughout the full extent of his immediate neighbors' territories, regardless of the singer's position in his own territory. This close relationship between active space of song and territorial dimensions suggests that the critical factor which influenced the evolution of song parameters that determine active space was the ability to communicate the signaller's presence to his neighbors at the furthest reaches of their territories. An interesting test of this hypothesis will be to compare active space and territory size in a variety of species occupying different habitats and having different territory sizes.

As discussed in the Introduction, active space is determined by 4 factors. Of these only signal amplitude, the masked auditory threshold, and, to some extent, the rate of signal attenuation are subject to change through evolutionary adaptation. The amplitude of ambient noise is an aspect of the environment.

The rate of signal attenuation can be influenced by the spectral and temporal structure of the signal. For long-range communication, however, there are rather severe environmental constraints that result in narrow windows of tolerance for these parameters (e.g. Morton 1975; Marten and Marler 1977; Marten et al. 1977; Wiley and Richards 1978; Bowman 1979; Richards and Wiley 1980; Brenowitz 1982). This has led to overall convergence in the range of frequency and temporal parameters in signals used over long distances in a given habitat.

In a natural habitat the maximum distance over which a signal can be detected will ultimately be set by that distance at which signal amplitude falls below the ambient noise level. Thus, even if a species has evolved an auditory system that is very sharply tuned to the frequency band in which signal energy occurs, and is therefore able to distinguish a masked signal at S/N ratios that approach zero, there is a distinct and unavoidable limit to sensitivity imposed by the environment.

Such considerations imply, therefore, that the determinant of active space which is most open to evolutionary modification is the amplitude at which the signal is produced. Since there is a definite energetic cost to singing (see Brackenbury 1979), especially when performed repeatedly over a day, and since the cost rises with increasing amplitude, we might expect maximum amplitude of production to be set at a level that will insure that the active space encompasses the extent of the neighbors' territories. If, in fact, song amplitude is related to territorial dimensions, then it can be predicted that amplitude should not be passively determined solely by body weight. This might be anticipated a priori from the observation that the ultimate source of power is the respiratory muscles which increase in size and power with body weight.

To test this prediction, I calculated the Spearman rank correlation coefficient between song SPL and body weight using data for 17 songbird species from Brackenbury (1979, Table 1) and for redwings from the present study. There is only a weak, though significant, correlation between these factors ($r_s = 0.57$, $P < 0.01$). The low parametric coefficient of determination ($r^2 = 0.354$) indicates that only about 1/3 of the observed variation in song SPL is accounted for by body weight. This is graphically demonstrated by the observation that the European Wren (*Troglodytes troglodytes*), which weighs about 10 g, sings at about 90 dB SPL at 1 m, whereas the European Blackbird weighs about 96 g but only sings at a maximum SPL of 87 dB. These values must be interpreted with caution, however, since they are based on measurements from single birds and song SPL may vary with aggressive arousal or other factors.

An alternative approach to this question is to attempt to predict, using data from the present study on the other determinants of active space, the song amplitude that would result in an effective distance that encompasses the maximum distance across 2 territories. In making this prediction the regression equation measured in the absence of wind from Table 1 was used:

$$Y = -66.69 + 3.39X$$

Y was set equal to 160 m, the upper limit to the maximum distance across 2 redwing territories, and was considered, then, to be the distance over which song amplitude attenuated from a maximum level (to be predicted) to a value 3 dB above the ambient noise level. X represented this total attenuation in song SPL. The overall mean of the measured hourly mean ambient noise levels was used in making this prediction, and was equal to 22.02 dB SPL. Solving the regression equation with these values resulted in a predicted maximum song SPL of 91.9 dB. The predicted value falls within the measured song SPL range of 88.5–93.5 dB and is very close to the measured mean of 90.8 dB SPL. This supports the idea that the ability to communicate a territory owner's presence throughout his neighbors' territories was of great selective value in the evolution of signal design features that determine the effective distance.

To my knowledge this study presents the first quantitative determination of active space for an acoustic signal. It seems quite likely, however, that studies with other birds will similarly demonstrate a relationship between active space and territorial dimensions. Studies of this kind need not be limited to territorial song in birds, however. Acoustic signals in general can be expected to evolve so that their active spaces are related to distances relevant to the communicatory function served by the signal and the social system of the species in question. Future investigations could use similar methods to study acoustic communication systems in a wide distribution of vertebrate and arthropod species.

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Appendix

Ambient noise levels ($\bar{X} \pm$ SE) measured on a linear unweighted scale each h from dawn to dusk on one day in the breeding season.

Time (h)	Ambient noise level (dB SPL)
05:20	47.9 ± 0.32
06:00	55.2 ± 0.22
07:00	57.0 ± 0.24
08:00	54.1 ± 0.28
09:00	57.6 ± 1.06
10:00	58.8 ± 0.72
11:00	66.8 ± 0.97
12:00	59.9 ± 1.06
13:00	68.8 ± 1.22
14:00	72.6 ± 1.09
15:00	68.3 ± 0.79
16:00	70.1 ± 0.79
17:00	71.4 ± 1.02
18:00	75.7 ± 1.04
19:00	60.4 ± 0.64
20:00	53.0 ± 0.27
20:20	52.4 ± 0.30

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