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GENERAL BIOLOGY

Vocal Activity of the Red Deer and the Acoustic Structure of Its Rutting Calls in the Russian Far East

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The red deer *Cervus elaphus* has established as a species in Central Asia, in the Tarim Basin, approximately two million years ago and spread from this basin in two branches. The western branch went through the Caucasus and Carpathian Mountains to Western Europe, and the eastern branch passed the Tien Shan, Altai, and Siberia to eventually reach North America [1–3]. Within the current distribution range covering the overall Holarctic, this species has many subspecies, which differ from each other not only in their size and morphology, but also in the stag rutting calls [1, 2]. The stags of the European subspecies—Scottish *C. e. scoticus* [4], Corsican *C. e. corsicanus* [5], and Spanish *C. e. hispanicus* [6, 7]—have low-frequency rutting calls. However, characteristic of the stags of Siberian and North American subspecies—Altai wapiti *C. e. sibiricus* [1, 8], Canadian wapiti *C. e. canadensis* [9], and Roosevelt elk *C. e. roosevelti* [10]—are high-frequency rutting calls, referred to as bugles.

The rutting calls of another subspecies, the Bactrian deer *C. e. bactrianus*, living in the center of species origin, have both low and high basic frequencies, which may occur both separately and in combination [1]. Thus, the Central Asian Bactrian deer subspecies comprises two frequencies in its rutting call, in contrast to the western and eastern subspecies with their rutting calls of only low and only high basic frequencies, respectively. Such a wide variation in the rutting call structure may be regarded as a natural experiment on the evolution of communicative behavior. A subspecific variation in the stag rutting calls has long been known [1]; however, the evolutionary factors responsible for this variation are still unclear, as well as the mechanisms, morphological or acoustic, underlying these calls. There are yet no data on how these rutting calls develop in ontogenesis in different subspecies of the red deer. Thus, it is necessary to consolidate the data on the acoustic structure, sex-dependent specific features, ontogenesis, morphology, and physiology of the vocal systems of different subspecies. Of special interest in this perspective are the Siberian subspecies, namely, the Altai wapiti and the red deer subspecies *C. e. xanthopygus*, northeastern red deer, well distinguishable with the help of genetic markers [3]. However, their vocal behavior is poorly studied as compared with the European and American red deer subspecies; the structure of Altai wapiti rutting call has been described in a few papers [1, 8]; as for the *C. e. xanthopygus,* only one spectrogram of its rutting call is available without any detailed description of its acoustic structure [1].

Deer census by voice is frequently used as a characteristic of the animal abundance. Game managers use one or several voice counts per rutting season, but they may not coincide with the rut peak [11]. Automated recording systems may be useful for validation of aural deer censuses. Such systems operate in an autonomous manner, without involvement of any personnel, following a specified schedule, day and night, and day after day. This provides long-term records over the entire season in order to assess the dynamics of vocal activity in deer populations [8, 12].

The goal of this study, performed using automated audio recorders, was to clarify the dependence of vocal rutting activity of the stag northeastern red deer on the time of day and ambient temperature and to preliminarily describe the structure of stag northeastern red deer rutting calls as compared to the rutting calls of other red deer subspecies.

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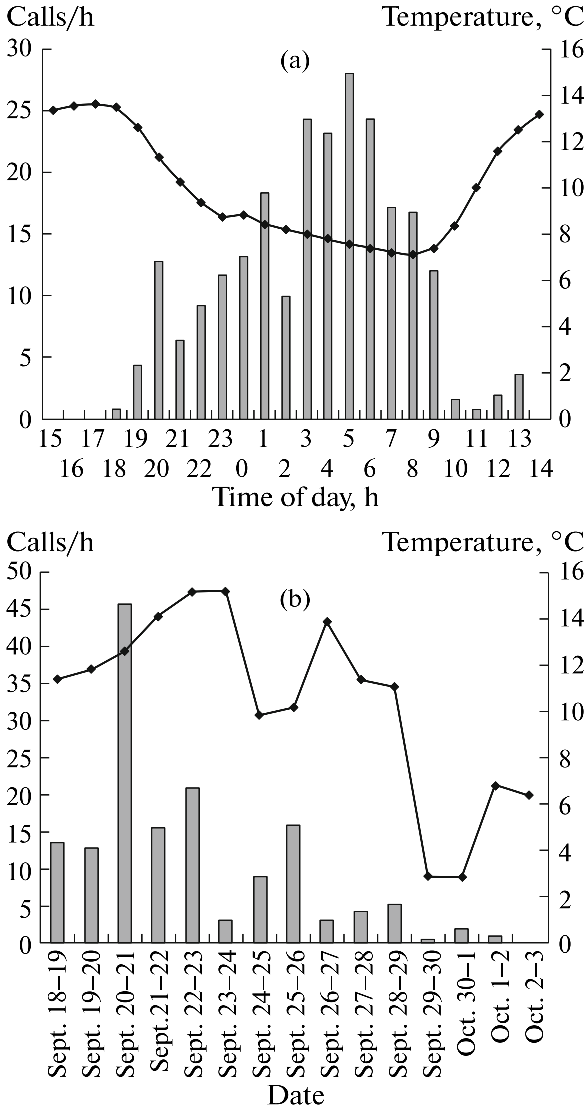

Fig. 1. Dynamics of the red deer rutting roar (calls/h, columns) and ambient temperature (line) depending on (a) time of the day and (b) calendar date.

MATERIALS AND METHODS

The material was recorded from September 18 to October 16, 2014, in the eastern part of the Komarov Ussuriiskii State Nature Reserve, Far East Branch, Russian Academy of Sciences. The sound (22.05 kHz, 16 bits, stereo) was recorded with six SongMeter SM2+ (Wildlife Acoustics, United States) automated audio recorders with two circular microphone arrays located at an angle of 180° relative to each other. The recorders were installed along the Suvorovka and Karyavaya river valleys with a minimal distance of 1 km between them. Two recorders were stationary, while the remaining four devices were moved to different sites to elevate the probability for recording red deer calls.

Records were made on a daily basis using the following schedule: 5-min recordings and a 25-min interval for all six recorders; totally, 4 h of record per device. This mode allowed the calculation of the rutting activity dynamics according to days and parts of the day. In order to exclude simultaneous recording of the same call, the recording periods for adjacent recorders were desynchronized. During the recording, the devices also determined the air temperature (every 5 min). In addition, over the period of September 29–October 16, the recorders were additionally switched on from 7 p.m. to 7 a.m. in the intervals between the main records; this gave an additional 9 h of records for the period of the maximum acoustic activity (nighttime) per each recorder. The total duration of all records is 880 h.

In order to assess the rutting activity dynamics for a 15-day period (3 p.m., September 18 to 3 p.m., October 3) with the help of the Avisoft SASLab Pro software (Avisoft Bioacoustics, Germany), all the rutting calls recorded at the watershed of the Suvorovka and Karyavaya rivers (43°39′11″ N, 132°38′38″ E) independently of their quality, including the faint sounds

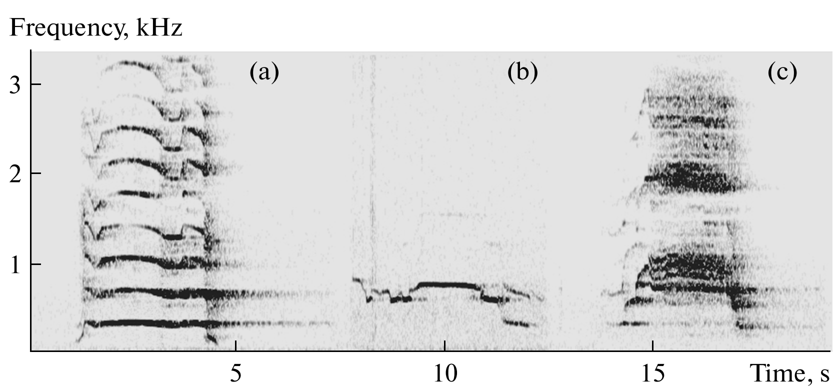

Fig. 2. Spectrograms of three red deer rutting calls recorded with the help of a SongMeter recorder: (a) low-frequency call; (b) high-frequency call; and (c) high-frequency call with a chaotic segment. The spectrograms are constructed using a sampling frequency of 11.025 kHz, Hamming window, FFT length of 1024, frequency frame of 50%, and time overlap of 75%.

indistinguishable in the overall noise but detectable with the PC, were counted. The total sample comprised 611 calls. The number of recorded calls for each hour of record made it possible to compute the daily rutting call dynamics over the 15-day period (according to the daily mean values and totally for all 24 h of records), as well as the dynamics on an hourly basis for the day (according to the mean values for an hour, totally for all 15 days). The average ambient temperature was calculated for each hour; its daily and hourly dynamics were calculated in the same manner.

In order to describe the structure of the rutting calls of northeastern red deer stags, 202 high-quality calls were selected. The duration of each call was measured with the use of Avisoft SASLab Pro, as well as the maximum and minimum basic frequencies in the spectrogram window constructed using a sampling rate of 11.025 kHz, Hamming window, FFT length of 1024, frequency frame of 50%, and time overlap of 93.75%.

The Statistica software package (StatSoft, United States) was used for data processing; the results are shown as $\bar{X} \pm SD$. The temperature effect on the rutting call dynamics was assessed using the Pearson correlation coefficient. The joint effect of ambient temperature, hour of the day, and recording date on the rutting activity (number of calls per hour) was estimated using MANOVA (GLM), with the hour of the day and recording date as categorical variables and temperature as a continuous variable.

RESULTS AND DISCUSSION

The maximum number of calls per hour was observed in the nighttime (3 a.m. to 6 a.m.), whereas the period from 2 p.m. to 5 p.m. was completely free of rutting calls (Fig. 1). The rutting calls of northeastern red deer were two times less frequent in the first half of dark time (8 p.m. to 1 a.m.) as compared with the second half (2 a.m. to 7 a.m.), namely, 11.9 versus 21.2 calls per hour. The number of calls per hour was negatively correlated (in a statistically significant manner) with the ambient temperature ($r = -0.79$, $p < 0.001$, $n = 24$).

Since the northeastern red deer stags were silent in the middle of the day, we divided the period of records into 15 conditional days starting from 3 p.m. and ending at 2 p.m. of the next day (Fig. 1). The number of calls during the first seven nights (September 18–25) was four times larger (on average, 17.35 calls/h) as compared with the subsequent seven nights (September 25–October 2; on the average, 4.57 calls/h). Any calls were absent during the 15th night. The maximum number of calls, amounting to 47.75 calls/h, was recorded during the third night (September 20–21). The number of calls displayed a positive correlation with the average daily temperature; however, this correlation was below the significance threshold ($r = 0.44$, $p = 0.10$, $n = 15$).

Since the ambient temperature depended on both the part of the day and date of recording, we estimated the joint effect of these three factors on the number of rutting calls per hour using MANOVA. All three factors had a statistically significant effect on the rutting activity of northeastern red deer; the effects of ambient temperature ($F_{1,\,321} = 26.7$, $p < 0.001$) and the date of recording ($F_{14,\,321} = 14.6$, $p < 0.001$) were more pronounced as compared with the time of the day ($F_{23,\,321} = 2.0$, $p = 0.004$).

Comparison of these data with the results of other studies has demonstrated that the time of the day and temperature may have different effects on the rutting vocal activity of red deer. In the Alpine population (Italy), stags mainly roared in the night and early morning (5 a.m. to 7 a.m.) [13]. However, the stags of the Isle of Rum red deer [14] roared mainly during daytime, as did farmed red deer stags in France [15]. The calls of Altai wapiti in a wildlife population were uniformly recorded during the night with a small increase by dawn time [8]. The diurnal cycles of stag vocal activity in two farmed Altai wapiti populations in Central Russia also differed: the stags of the first population roared during the dark time (6 p.m to 9 a.m.) and of the second, mainly near 9 a.m. and 5 p.m. during feeding [12].

Unlike our results, a study of the Altai wapiti in two farmed populations failed to find any statistically significant effect of the ambient temperature on the number of ratting calls, as well as of the season and part of the day [12]. The effect of temperature on the vocal activity of stags in the wildlife Alpine population was also absent [13], while a 31-year study in France has demonstrated a negative correlation between ambient temperature and the counted rutting calls. This is explainable by a decrease in animal activity with increase in temperature [11]. Similarly, a study of the rutting activity in free-living Altai wapiti has found a negative correlation between the number of calls and ambient temperature [8].

Most rutting sounds by northeastern red deer are solitary cries (Fig. 2), and only sometimes a main (longer) call is followed by one or several shorter cries. The average duration of main calls was 3.41 ± 0.65 s, varying in the range of 1.46 to 4.95 s. The maximum basic frequency on the average amounted to 0.66 ± 0.15 kHz (1.01–0.32 kHz) and minimum basic frequency, 0.19 ± 0.05 kHz (0.09 to 0.44 kHz).

The duration of the rutting calls of northeastern red deer is similar to that of Altai wapiti, Khakassian red deer, and wapiti in North America, which also mainly use single high-frequency calls during rutting. The duration of the rutting calls by Khakassian red deer varies from 2.09 to 4.63 s, averaging at 3.1 s [8] and of the Altai wapiti, as a rule, does not exceed 2–3 s [1], being slightly shorter in the case of the Canadian wapiti (2.4–2.9 s) [9]. On the other hand, the ratting call by the stags of European red deer subspecies is considerably shorter, namely, 1.8 s for the Corsican subspecies [5], 1.9 s for the Scottish subspecies, and 2.0–2.5 s for the Spanish subspecies [6, 7]. Only the upper boundary of call duration of the Spanish subspecies [6] reaches the average values characteristic of the northeastern red deer (3.8 s).

The basic frequency in the northeastern red deer rutting calls (0.66 kHz) is considerably lower as compared with the Canadian wapiti (2 kHz) [9] or Roosevelt elk (over 1.5 kHz) [10]. The average maximum basic frequency in the calls of Khakassian red deer (1.23 kHz [8]) is also almost twofold higher as compared with the northeastern red deer, although the most high-frequency northeastern red deer calls (1.01 kHz) overlap in frequency with the lowest Khakassian red deer calls (0.79 kHz). The lower boundary of the maximum basic frequency for the northeastern red deer (0.32 kHz) coincides with the highest values of the maximum basic frequency in the calls of the Spanish subspecies (0.34 kHz [6]), whose rutting calls are the highest among all the European red deer variants [6, 7]. The minimum basic frequency of the northeastern red deer calls is also intermediate between the average values for the Altai wapiti (0.29 kHz [8]) and the Spanish subspecies (0.11–0.12 kHz [6, 7]).

Thus, the rutting calls of northeastern red deer stags have the lowest frequency among those of all eastern red deer subspecies although considerably higher as compared with any of the western subspecies. Considerable differences in the rutting call frequency between the Altai wapiti and northeastern red deer allows these calls to be used a diagnostic subspecific character along with specific morphological and genetic features of these subspecies. Clarification of the evolutionary causes underlying a wide variation in the rutting vocal demonstrations of the red deer stags requires more comprehensive studies of the acoustic characteristics and rates of different basic frequency modulation patterns in the rutting calls of individual subspecies.

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