



Daurian pika (*Ochotona dauurica*) alarm calls: individual acoustic variation in a lagomorph with audible through ultrasonic vocalizations

ILYA A. VOLODIN,^{*,} ELENA V. VOLODINA,[°] ROLAND FREY,[°] KSENIYA D. KARASEVA, AND VADIM E. KIRILYUK

Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow 119234, Russia (IAV, KDK)
Department of Behaviour and Behavioural Ecology of Mammals, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia (IAV, EVV)

Department of Reproduction Management, Leibniz Institute for Zoo and Wildlife Research, Berlin 10315, Germany (RF)
Daurian State Nature Biosphere Reserve, Nizhnii Tsasuchei, Ononskii District, Zabaikalskii Krai 674480, Russia (VEK)
Department of Biogeography, Institute of Geography, Russian Academy of Sciences, Moscow 119017, Russia (VEK)

* Correspondent: volodinsvoc@gmail.com

Colonial lagomorphs warn conspecifics of potential danger with alarm calls encoding information about attributes of presumptive predators as well as the caller. In this study, we show that alarm calls of Daurian pikas, *Ochotona dauurica* (Pallas, 1776), encode information about caller identity. We recorded the alarm calls produced toward a surrogate predator (researcher), slowly moving (0.5–1 km/h) between densely distributed colonies. The alarm calls of most (32 of the 35) callers started in the ultrasonic range at 22.41 kHz on average and rapidly decreased to 3.88 kHz on average at call end. Call duration was very short (0.057 s on average). The accuracy of classifying alarm calls to correct callers with discriminant function analysis (DFA) was 93.71% for the manually measured set of 12 acoustic variables and 95.43% for the semiautomatically measured set of 12 acoustic variables; in both cases exceeding the level of chance (17.28% or 17.33%, respectively). Nonlinear vocal phenomena (biphonations) only were detected in one individual. We discuss the relationship between vocal traits, individuality, vocal production mechanisms, and functions, of pika alarm calls. We propose a potential divergence of alarm calls in Asian pikas to high-frequency whistles (> 20 kHz in Daurian pikas) and in American pikas to low-frequency emissions (0.4–1.3 kHz in *Ochotona princeps*) during the evolutionary radiation of pikas at the center of the origin of lagomorphs in East Asia and their subsequent geographic dispersal.

Keywords: acoustic variables, alarm call, audible vocalization, individual differences, Lagomorpha, mammal, manual and semiautomatic measurements, pika, ultrasonic frequency range

Acoustic variation of alarm calls, including individual vocal signatures, may prove adaptive in reducing predation risk (Sherman 1977; Blumstein 2007; Sloan and Hare 2008; Fallow et al. 2013; Engesser et al. 2019). Individual-specific alarm calls have been reported for many colonial mammals (Blumstein and Munos 2005; Matrosova et al. 2009, 2010a, 2010b; Schneiderová and Policht 2010; Schneiderová et al. 2017), and listeners can discriminate callers by their alarm calls (Hare 1998; Frommolt et al. 2003; Blumstein et al. 2004).

Individualized alarm calls serve many functions in relation to antipredator behavior (Pollard 2011). Individual vocal signatures allow receivers to discern between approaching versus

retreating predators (Thompson and Hare 2010), as they provide cues to the number of callers (Weary and Kramer 1995; Sloan and Hare 2008), caller reliability (Hare and Atkins 2001; Blumstein et al. 2004), and colony membership or familiarity (Conner 1985a; Volodin et al. 2018). Colonial territorial mammals communicate predator approach by increasing the alarm call rates (Ivins and Smith 1983; Blumstein and Armitage 1997; Warkentin et al. 2001). Despite this, playback studies have revealed that communicating predator movements via changes in call rate only is possible if the alarm calls are individualistic and can be discriminated by receivers (Wilson and Hare 2003; Thompson and Hare 2010). In addition, high-arousal

individualized vigilance calls are used outside the context of mobbing predators, for example, during aggressive encounters while defending a territory (Matrosova et al. 2012), while defending wintering food stores (Volodin et al. 2018) or during mate guarding (Tamura 1995; Manno et al. 2007).

In colonial ground-dwelling mammals, individual vocal signatures have been documented in very simple-structured alarm calls (Conner 1982; Matrosova et al. 2009) as well as in moderately complex (Matrosova et al. 2010a) or very complex alarms (Schneiderová and Policht 2010; Schneiderová et al. 2017; Volodin et al. 2018). If vocal complexity is not critically important for encoding individuality, the question arises, why are alarm calls so variable and complex in ground-dwelling rodents (Matrosova et al. 2011; Schneiderová et al. 2017) and lagomorphs (Lissovsky 2005; Borisova et al. 2008; Volodin et al. 2018). In most other mammals and birds, alarm calls have a simple inverse-U (“chevron”) or flat contour (Morton 1977; Randall and Rogovin 2002; Frommolt et al. 2003; Cäsar et al. 2012; Volodina et al. 2018; Engesser et al. 2019).

Among Lagomorphs, hares and rabbits (Leporidae) mostly are silent (Rehnus et al. 2019), whereas pikas (Ochotonidae) are very vocal. Beyond alarm calls (synonym: “short calls”), *Ochotona* species produce trills (synonym: “long calls”) and songs. The main function both of trills and songs is defending the territory of a family-based breeding colony (Conner 1985b, Nikolskii et al. 1990; Kojima et al. 2006; Borisova et al. 2008). This function of songs and trills is shared with the role of the alarm calls in territorial maintenance against conspecific intruders (Conner 1984; Smith and Ivins 1984). However, whereas alarm calls are produced by immobile animals (Volodin et al. 2018), songs and trills mainly are produced by moving pikas (Proskurina 1991). Alarm calls and trills are produced by both sexes, whereas songs are produced by males only (Borisova et al. 2008).

In all studied *Ochotona* species, alarm calls are individual-specific and therefore can serve as acoustic markers of individual callers to conspecifics. For example, individual-specific alarm calls were found in four male American pikas *Ochotona princeps*, and playbacks confirmed that recipient American pikas discriminated between the alarm calls of familiar and unfamiliar individuals (Conner 1985a). Individual-specific alarm calls also were found in the Altai pika *Ochotona alpina* among 38 individual callers (Volodin et al. 2018). In Daurian pika *Ochotona dauurica*, individuality of alarm calls has yet to be investigated.

Potentially, a trade-off between the individualistic and propagation traits is related to alarm call frequency range and contour shape (Titze and Palaparthi 2018). Both acoustic traits vary considerably among *Ochotona* species. The fundamental frequency (f_0) of the alarm calls does not correlate with a species' body size: the comparably sized Daurian pika and American pika produce alarm calls differing up to 15 times in maximum f_0 . The sweep-like alarms of Daurian pikas (body mass 103 – 190 g—Lissovsky 2016) rapidly fall from 16 to 3.5 kHz over a very short call duration of 0.02 – 0.04 s (Nikolskii et al. 1989; Borisova et al. 2008). In American pika (body mass 121 – 176

g—Smith and Weston 1990) alarm calls have a longer duration (0.13 – 0.40 s) and are substantially lower in frequency, with maximum f_0 being less than 1 – 2 kHz (Somers 1973; Conner 1982, 1985b). By comparison, the complex alarm calls of the largest-sized Altai pika (body mass 293 g—Westover and Smith 2020) have an intermediate duration of 0.073 – 0.157 s and a maximum f_0 of 7.31 – 15.46 kHz (Volodin et al. 2018). The alarm call contours also are substantially different among *Ochotona* species: they are rapidly descending in Daurian pika (*O. dauurica*—Nikolskii et al. 1989; Borisova et al. 2008), ascending in Mongolian pika (*O. pallasii*—Nikolskii et al. 1989), chevron-shaped in Altai pika (*O. alpina*), and Northern pika (*O. hyperborea*—Lissovsky 2005; Volodin et al. 2018), and slightly modulated or practically flat-contoured in American pika (*O. princeps*) and collared pika (*O. collaris*—Somers 1973; Conner 1982, 1985b; Trefry and Hik 2009, 2010).

Daurian pikas inhabit the steppes of South-East Russia, Mongolia, and North China (Komonen et al. 2003; Liao et al. 2006; Erbjeva et al. 2012). In the steppe ecosystems, Daurian pikas play an important role affecting plant richness and as prey of many predators (Komonen et al. 2003), especially for the Pallas's cat *Otocolobus manul*, for which Daurian pikas, disproportionately to their availability, are the most frequently consumed prey (Ross et al. 2010). From a bioacoustical point of view, the Daurian pika is interesting as a species producing the highest-frequency and the shortest alarm calls within the genus *Ochotona* (Nikolskii et al. 1989; Borisova et al. 2008).

The territory of a Daurian pika family-based colony (male, female, and young) may vary from 480 to 900 m², averaging 610 m² (Proskurina et al. 1985). Their burrow occupies 190 m² on average, with the number of burrow entrances varying from 10 to 180, (\bar{x} = 60—Olkova 1954). In August to September, family-based colonies mostly count 2.3 – 4.3 (range, 1 – 10) animals per burrow, sex ratio in population is approximately 1:1 (Olkova 1954). A radius of 32 m was used by Ross et al. (2010) to delineate the area defining 80% of the core area of a family-based colony in Daurian pikas. Daurian pika density varies strongly depending on habitats and year (Nekipelov 1954; Ross et al. 2010), as it does in other *Ochotona* species (Erb et al. 2014; Li et al. 2016; Volodin et al. 2018).

Previous studies have used manual measurements to analyze the acoustic structure of *Ochotona* alarm calls (Conner 1982, 1985a, 1985b; Nikolskii et al. 1990; Kojima et al. 2006; Borisova et al. 2008; Volodin et al. 2018). Despite the exclusive use to date of such manual measurement, currently available software for semiautomatic analyses seems well-suited for the very simple contours of the Daurian pika alarm calls (Arriaga et al. 2012; Ferhat et al. 2016; Dou et al. 2018). However, the results of different methods independently applied to the same call sample either may be in accord or differ, as has been shown for vocalizations of different laboratory strains of domestic mice *Mus musculus* (Binder et al. 2018, 2020). Manual measurements provide more precise results, so the automated methods need verification (Binder et al. 2020). In this study we therefore applied both manual and semiautomatic methods to the same sample of alarm calls of Daurian pikas. This allows

accrual of data that are comparable with previous studies of alarm call variation in *Ochotona* species. At the same time, we can compare the results of the traditional method with those of a more recent and less labor-intensive method. We examine acoustic variables and their potential to encode the individual identity of alarm calling Daurian pikas. An additional aim was to estimate whether the manual and semiautomatic methods for measuring acoustic variables with Avisoft SASLab Pro software provide the same or different results.

MATERIALS AND METHODS

Study site, dates, and specimens.—Alarm calls of wild adult unmarked Daurian pikas of unknown sex were recorded in Dauria, along the shore of the lake Zun-Torey and the wide isthmus between the lakes Zun-Torey and Barun-Torey (Transbaikalia, Russia, 50.06°N, 115.44°E), around the Teli field station, from 22 June to 16 July 2019. In summer 2019, both lakes were completely dried out. The study site is a grazing area used by wild Mongolian gazelles *Procapra gutturosa* and free-ranging herds of domestic livestock: sheep, horses, cattle, and domestic Bactrian camels (Volodin et al. 2017). The area is undulating at elevations of 600 – 1,100 m and the vegetation dominated by grass (Poales: Poaceae) species such as *Stipa* spp., *Cleistogenes* spp., and *Leymus* spp., several species of forbs, particularly *Artemisia* spp. (Asterales: Asteraceae), *Allium* spp. (Asparagales: Amaryllidaceae), and *Astragalus* spp. (Fabales: Fabaceae), and sedges, e.g., *Carex* spp. (Poales: Cyperaceae—Olson et al. 2005b; Kirilyuk 2007; Kirilyuk et al. 2018). Trees and bushes are lacking. Potential predators of Daurian pikas include: Pallas's cats; wolves, *Canis lupus*; corsac foxes, *Vulpes corsac*; red foxes, *V. vulpes*; and birds such as steppe and golden eagles (*Aquila rapax* and *A. chrysaetos*, respectively), upland buzzards (*Buteo hemilasius*), and cinereous vultures (*Aegypius monachus*—Olson et al. 2005a, 2005b; Kirilyuk et al. 2020). Data on Daurian pika population dynamics at this study site suggest considerable variation in population numbers from year to year (up to 20×) with a peak every 10 years (Nekipelov 1954). The most recent such population peak occurred in 2019.

In midsummer 2019, when our data were collected, Daurian pika family-based colonies were located along and between dirt roads crossing the area so that the study site represented a habitat extending for kilometers, with a very large numbers of family colonies of pikas available for recording alarm calls. The minimal distance among family-based colonies was ca. 30–50 m. Colonies contained both adults and pups born in the current year. Pups and adults were distinguishable by body size, as the pups were about half the size of the adults.

Acoustic recordings.—For acoustic recording (sampling rate 48 kHz, 16 bit resolution), we used three solid state digital recorders (Marantz PMD-660; D&M Professional, Kanagawa, Japan) with handheld microphones (Sennheiser K6-ME66; Sennheiser electronic GmbH & Co. KG, Wedemark, Germany), having a flat frequency response (± 2.5 dB) from 0.04 to 20 kHz. Acoustic recordings were made every day, primarily

in the morning and evening, during those hours in which the wind was weak and did not affect the recorded calls even when blowing directly to the microphone. Pikas produced alarm calls toward a standing or slowly moving (0.5–1 km/h) researcher. Recording started when a researcher heard alarm calls of pikas from a distance of 25 – 30 m (or sometimes spotted the caller) and directed the microphone toward the caller. After starting the recording, a researcher labeled the calls by voice (one, two, three, ...), to distinguish the calls of the focal caller from calls of other pikas from the same colony. Calls were considered as belonging to the focal caller when they came from a single spot and all were of the same intensity. While recording, the researcher approached step-by-step with pauses of 10 – 20 s and tried to see the caller. In 18 cases, when the researcher could see the caller, vocalizing pikas were adults; they were stationary near the burrow or partly inside the burrow. Pikas did not vocalize when moving. Recording lasted until the caller escaped to the burrow (commonly when the researcher reached distances of 4 – 5 m to the caller), or if the recording was interrupted by strong wind. After the end of the recording, the researcher moved slowly (0.5 – 1 km/h) to another colony; the precise speed of a researcher's movement and the number of stops for orientation toward the caller were not standardized.

To avoid repeated recording of the same animals, the area around the Teli field station was subdivided into sectors. Calls were recorded along transects extending radially in all directions up to a distance of 2 km from the field station. A researcher recorded calls alone, moving along a transect within a certain sector, and recording each colony only once. Thus, each alarm call series represented a recording session from one individual pika and was associated with a particular pika colony. The alarm calls of each focal individual were recorded as one audio file. Three researchers (IAV, EVV, and KVK), working independently, collected a total of 174 audio files from 174 different focal individuals. Previously, a similar approach for recording individual alarm call series of unmarked animals was used for ground squirrels (McCowan and Hooper 2002) and for Altai pikas (Volodin et al. 2018).

Call samples.—Selection of calls for analysis of acoustic variables and individual traits was done using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Only calls of good quality, not disrupted by wind and not overlapped by noise or other calls were included in the spectrographic analyses. For spectrographic analysis, we selected 35 audio files, including 35 series of alarm calls from 35 different focal individuals, one focal individual per colony. Each audio file contained at least 10 (from 10 to over 100) alarm calls. Calls of the remaining 139 pikas did not meet the quality and amount criteria outlined and were not included in the analyses. Of the 35 pikas selected to provide calls for analyses, 11 callers were visually observed by researchers.

We selected 350 alarm calls, 10 calls per individual, for measuring the acoustic variables. To reduce pseudoreplication, calls for measurements were selected from different parts of the series, but primarily from the end part, because, when a researcher approached a caller during recording, the distance

shortened and the last calls were of the best quality judged by signal-to-noise ratio. We have shown previously that selection of Altai pika alarm calls for analysis of individuality from different parts of a series (at the beginning, at the end, or randomly chosen) did not affect the results of the statistical analysis (Volodin et al. 2018).

Call analysis.—Before analysis, calls were high-pass filtered at 0.5 kHz to reduce the low-frequency background noise using Avisoft SASLab Pro, because a preliminary visual analysis of the spectrograms showed that call fundamental frequency always exceeded 1 kHz. In each of the 350 alarm calls, we carried out measurements of the acoustic variables applying two different methods: (i) the manual method by using different cursors in Avisoft and (ii) the semiautomatic method by using the “Automatic parameter measurements” option in Avisoft. In each call, we measured 12 acoustic variables manually and 12 variables automatically (Fig. 1).

Manual measurements.—We manually measured 12 acoustic variables (one temporal, five variables of fundamental frequency, and six power variables). Determining the onset of the alarm call is complicated in Daurian pika, because there is a very steady, smooth increase of expiration intensity at call

onset. We therefore determined the start and the end of a call by the appearance and disappearance of sound energy on a waveform (Fig. 1). Measurements of call duration were made with the standard marker cursor in the spectrogram window of Avisoft (sampling frequency 48 kHz, Hamming window, FFT 512 points, frame 50%, and overlap 96.87%; frequency resolution 94 Hz and temporal resolution of 0.33 ms). We measured the beginning ($f_{0\text{beg}}$) and end ($f_{0\text{end}}$) fundamental frequency with the free frequency cursor at the onset and end point of a call (Fig. 1). We then increased sound intensity and, by using the free moveable reticule cursor, measured the maximum ($f_{0\text{max}}$) and minimum ($f_{0\text{min}}$) fundamental frequencies (Fig. 1). The values of $f_{0\text{max}}$ could be higher than or equal to the value of $f_{0\text{beg}}$; the value of $f_{0\text{min}}$ could be lower than or equal to the value of $f_{0\text{end}}$. The value of call mean fundamental frequency ($f_{0\text{mean}}$) was calculated as average of 10 measurements of fundamental frequency, measured with equal intervals over the entire call duration from $f_{0\text{beg}}$ to $f_{0\text{end}}$ (see below).

Over the entire call power spectrum (between the onset and end point of a call), we measured f_{peak} , representing the value of the frequency of maximum amplitude, bandwidth of f_{peak} at the distance of -10 dB from the maximum (bnd) and the

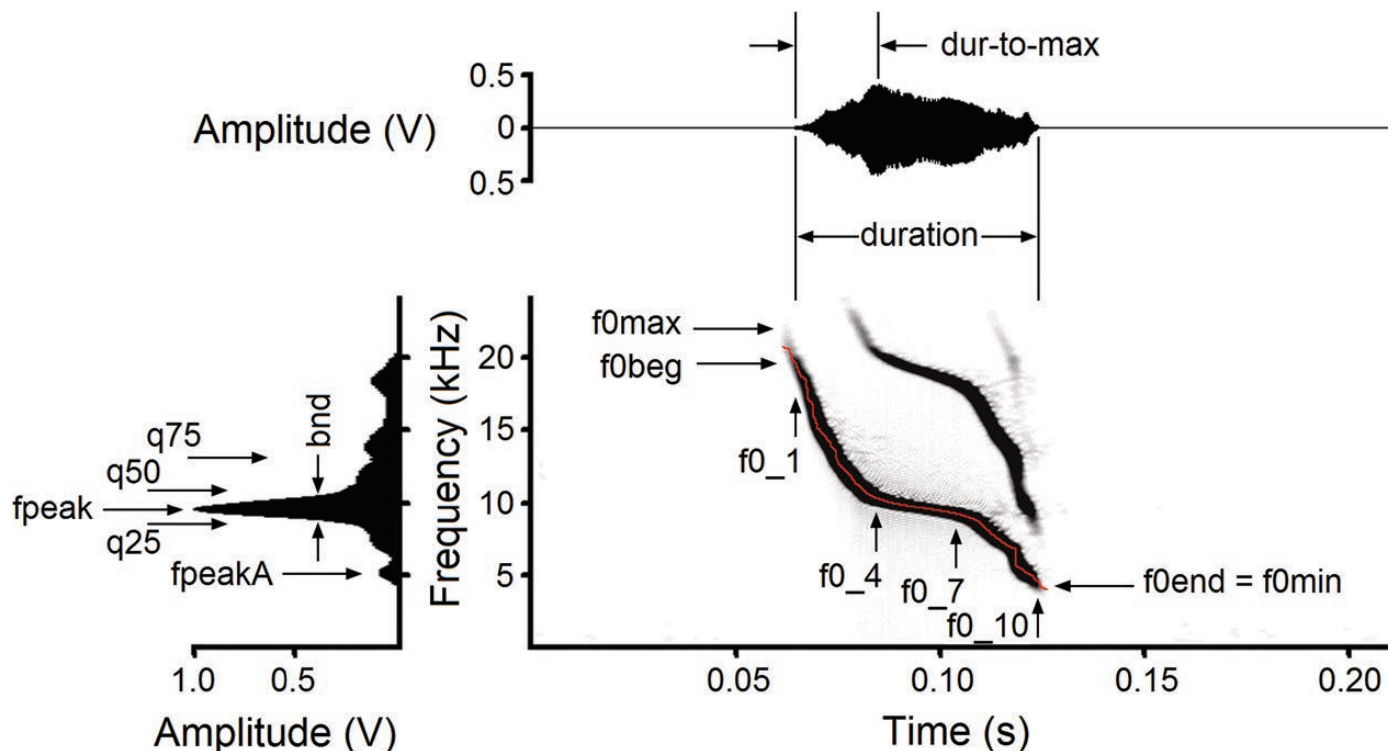


Fig. 1.—Waveform (above), mean power spectrum of the entire call (left), and spectrogram (right) indicate manually and semiautomatically measured acoustic variables of Daurian pika alarm calls. The mean power spectrum of the entire call was created between the two vertical lines in the waveform, marking the onset and end point of a call. The red line marks the track along which the semiautomatic measurements of fundamental frequency were made. Designations: duration—call duration; dur-to-max—duration from call onset to the point of maximum amplitude; $f_{0\text{max}}$ —the maximum fundamental frequency; $f_{0\text{min}}$ —the minimum fundamental frequency; $f_{0\text{beg}}$ —the fundamental frequency at the onset of a call; $f_{0\text{end}}$ —the fundamental frequency at the end of a call; $f_{0_1} = f_{0\text{beg}}$, f_{0_4} , f_{0_7} , $f_{0_{10}} = f_{0\text{end}}$ —four of 10 points for automatic measurements of the fundamental frequency at uniform intervals; f_{peak} —the frequency of maximum amplitude within a call; q_{25} , q_{50} , q_{75} —the lower, the medium, and the upper quartiles, covering, respectively, 25%, 50%, and 75% energy of a call spectrum, bnd —bandwidth of peak frequency; f_{peakA} —the frequency of the first power peak. The spectrograms were created with a Hamming window, 48 kHz sampling rate, FFT 512 points, frame 50%, and overlap 96.87%.

q25, q50, and q75, representing the lower, median, and upper quartiles, covering 25%, 50%, and 75% of the energy of the call spectrum, respectively (Fig. 1). Over the entire call power spectrum, we also measured the value of the first power peak (fpeakA); it was well visible in all calls, but its value always was substantially lower than those of fpeak (Fig. 1). All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, Washington).

Semiautomatic measurements.—We semiautomatically measured 12 acoustic variables (two temporal and 10 sequential measurements of fundamental frequency). To undertake these measurements, we visualized the track of the peak frequency in a call spectrogram and also cleaned the spectrogram by using the eraser cursor, thus deleting nontarget noise and intense fragments of the first harmonic. The resulting track of the peak frequency lay entirely on the fundamental frequency band of a call (Fig. 1). Then, using the automatic parameter measurements option in Avisoft including export of the results to Excel, we measured call duration (within the limits set by the standard marker cursor) and duration from call onset to the point of a call maximum amplitude (dur-to-max), as well as 10 measurements along the fundamental frequency track with equal intervals from call onset to call end. Because call duration during the automatic measurements corresponded to call duration during manual measurements, the first point of the f0 measuring (f0_1) corresponded to f0beg of the manual measurements; the last point of measuring the f0 (f0_10) corresponded to f0end of the manual measurements; and the remaining eight f0 measurements (from f0_2 to f0_9) were made automatically at uniform intervals equal to 1/9 of the entire call duration (Fig. 1). We then calculated the duration from call onset to the point of the call maximum amplitude in terms of the percentage of the entire call duration (dur-to-max%) and used these values within the statistical analyses.

In each call, we also scored presence/absence of nonlinear vocal phenomena (Wilden et al. 1998; Frey et al. 2016), following similar analyses applied in a previous study of Altai pika alarm calls (Volodin et al. 2018). We scored the presence of particular nonlinear vocal phenomena only in those cases where call portions containing this nonlinear phenomenon exceeded 10% of the total call duration.

Statistics.—Statistical analyses were carried out using STATISTICA v. 8.0 (StatSoft, Tulsa, Oklahoma) and R v. 3.0.1 (R Core Team 2013). Means are given as mean \pm SD, all tests were two-tailed, and differences were considered significant whenever $P < 0.05$. Distributions of all measured parameter values did not depart from normality (Kolmogorov–Smirnov test, $P > 0.05$) and met the assumption of homogeneity of variance (Levene's test, $P > 0.05$).

We used a one-way ANOVA in STATISTICA, to compare within- and between-individual variation of acoustic parameter values separately for the 12 manually measured and for the 12 semiautomatically measured acoustic variables. We used discriminant function analysis (DFA) in STATISTICA, to calculate the probability of the assignment of calls to the correct individual separately with the 12 manually measured or with

the 12 semiautomatically measured acoustic variables. The DFA standard procedure in STATISTICA includes a built-in option which tests variables for correlatedness and does not allow including the highly correlated variables in the analysis. All variables used met the criteria for inclusion in DFA.

For validation of DFA results, we used half-and-half cross-validation on the basis of even (training set) and odd (test set) order numbers of the calls of each individual. The training set contained 175 alarm calls, five per individual, from 35 study animals. The test set contained the remaining 175 alarm calls, five per individual, from 35 study animals. DFA for the test set was carried out using discriminant functions, calculated by the acoustic variables of the calls from the training set.

We used values of Wilks' Lambda to estimate how strongly the acoustic variables of the calls contribute to the discrimination of individuals. We used a repeated measures ANOVA to compare the values of correct assignment of calls to individual callers among DFAs. To validate our DFA results, we calculated the random values of correct assignment of calls to individual callers on the entire sample of 350 alarm calls by applying randomization procedures with macros created in R. The random values were averaged from DFAs carried out on 1,000 randomized permutations on the data sets as described by Solow (1990). For example, to calculate the random value of classifying alarm calls to individual pikas, each permutation procedure included the random permutation of 350 calls among 35 randomization groups corresponding to the 35 individual pikas, which were examined, followed by the DFA standard procedure in STATISTICA. All other permutation procedures were made similarly. Using a distribution obtained by the permutations, we noted whether the observed value exceeded 95%, 99%, or 99.9% of the values within the distribution, establishing that the observed value differed significantly from chance with a probability $P < 0.05$, $P < 0.01$, or $P < 0.001$, respectively (Solow 1990; Sibiryakova et al. 2015; Volodin et al. 2018).

RESULTS

Alarm call acoustics.—The alarm calls of Daurian pikas were of very high frequency and very short duration (0.057 ± 0.012 s; Table 1). In all individuals, the f0 was maximal at the beginning of a call (f0max = 22.41 ± 1.56 kHz) and rapidly decreased to the lowest value at the end of a call (f0min = 3.88 ± 0.29 kHz). The descending sweep-like shape of the fundamental frequency contour was uniform across all individuals (Fig. 2). In most individuals (32 of 35), calls started in the ultrasonic range of frequencies (> 20 kHz), then extended into the audible range. The peak frequency (fpeak = 9.89 ± 0.73 kHz) was located approximately at the center of the call frequency range. The point of call maximum amplitude was shifted toward call end ($66.1 \pm 11.3\%$). One-way ANOVA revealed pronounced individual differences for both manually and semiautomatically measured acoustic variables of the alarm calls (Table 1).

Nonlinear vocal phenomena only were found in 10 alarm calls of one of the 35 individuals. All 10 alarm calls of this animal contained the nonlinear phenomenon biphonation: two

Table 1.—Mean \pm SD and min–max values for acoustic variables of the alarm calls of 35 Daurian pikas (calculated as average of within-individual averages), and one-way ANOVA results for individual differences. m = variable from the set of manually measured parameters; sa = variable from the set of semiautomatically measured parameters; n = number of animals.

| Alarm call variable | Set | Mean \pm SD (n = 35) | Min–max (n = 35) | ANOVA |
|---------------------|-------|------------------------|------------------|---------------------------------|
| duration (ms) | m; sa | 57.2 \pm 11.7 | 39.7 – 87.9 | $F_{34,315} = 105.6, P < 0.001$ |
| dur-to-max% (%) | sa | 66.1 \pm 11.3 | 37.9 – 82.0 | $F_{34,315} = 35.9, P < 0.001$ |
| f0beg = f0_1 (kHz) | m; sa | 21.35 \pm 1.52 | 16.73 – 23.29 | $F_{34,315} = 61.3, P < 0.001$ |
| f0_2 (kHz) | sa | 17.72 \pm 1.63 | 14.14 – 21.21 | $F_{34,315} = 89.3, P < 0.001$ |
| f0_3 (kHz) | sa | 15.50 \pm 1.76 | 11.93 – 19.40 | $F_{34,315} = 158.8, P < 0.001$ |
| f0_4 (kHz) | sa | 13.86 \pm 1.74 | 10.34 – 18.34 | $F_{34,315} = 177.1, P < 0.001$ |
| f0_5 (kHz) | sa | 12.50 \pm 1.78 | 9.36 – 17.27 | $F_{34,315} = 195.7, P < 0.001$ |
| f0_6 (kHz) | sa | 11.40 \pm 1.65 | 8.39 – 15.82 | $F_{34,315} = 183.8, P < 0.001$ |
| f0_7 (kHz) | sa | 10.19 \pm 1.37 | 7.04 – 13.85 | $F_{34,315} = 155.0, P < 0.001$ |
| f0_8 (kHz) | sa | 8.70 \pm 1.06 | 5.49 – 11.26 | $F_{34,315} = 42.3, P < 0.001$ |
| f0_9 (kHz) | sa | 6.31 \pm 1.04 | 4.83 – 8.64 | $F_{34,315} = 65.1, P < 0.001$ |
| f0end = f0_10 (kHz) | m; sa | 4.01 \pm 0.29 | 3.52 – 4.91 | $F_{34,315} = 33.9, P < 0.001$ |
| f0max (kHz) | m | 22.41 \pm 1.56 | 16.90 – 23.90 | $F_{34,315} = 55.7, P < 0.001$ |
| f0min (kHz) | m | 3.88 \pm 0.29 | 3.41 – 4.70 | $F_{34,315} = 28.7, P < 0.001$ |
| f0mean (kHz) | m | 12.10 \pm 1.13 | 9.75 – 15.21 | $F_{34,315} = 145.1, P < 0.001$ |
| fpeak (kHz) | m | 9.89 \pm 0.73 | 8.97 – 12.74 | $F_{34,315} = 7.78, P < 0.001$ |
| q25 (kHz) | m | 8.87 \pm 0.64 | 7.27 – 9.86 | $F_{34,315} = 25.0, P < 0.001$ |
| q50 (kHz) | m | 10.67 \pm 0.85 | 9.38 – 12.37 | $F_{34,315} = 35.4, P < 0.001$ |
| q75 (kHz) | m | 13.03 \pm 1.05 | 10.51 – 14.97 | $F_{34,315} = 38.7, P < 0.001$ |
| bnd (kHz) | m | 3.49 \pm 1.58 | 1.35 – 7.43 | $F_{34,315} = 12.6, P < 0.001$ |
| fpeakA (kHz) | m | 5.16 \pm 0.40 | 6.16 – 4.40 | $F_{34,315} = 78.0, P < 0.001$ |

independent fundamental frequencies, a high (f0) and a low (f0low), interacting with each other and thereby generating combinatory frequency bands (Fig. 2). In this particular individual, the high fundamental frequency decreased from maximal values at the start of a call (20.41 \pm 0.53 kHz) to minimal values of 4.08 \pm 0.19 kHz at the end of a call. In all 10 alarm calls, the low fundamental frequency always appeared from the midpoint of call duration and continued to the end of a call, occupying 59.4 \pm 5.6% of the entire call duration. The low fundamental frequency decreased from the maximal values of 1.64 \pm 0.08 kHz at its appearance to minimal values of 0.82 \pm 0.17 kHz at the end of a call.

A preliminary visual inspection of a large number of spectrograms of the alarm calls indicated that only some calls to a small extent exceeded the highest frequency limit of the recording equipment used beyond the upper frequency limit of 24 kHz. This could be evaluated by the aliasing effect, discernable as a mirror reflection of the frequencies exceeding the upper frequency limit (24 kHz) down to the lower-frequency range (below 24 kHz). The aliasing effect in the alarm calls of the Daurian pikas was usual for harmonics but very rare for the uppermost parts of the fundamental frequency band. This means that the upper limit of the maximum fundamental frequency of the alarm calls of Daurian pikas approximately coincides with 24 kHz.

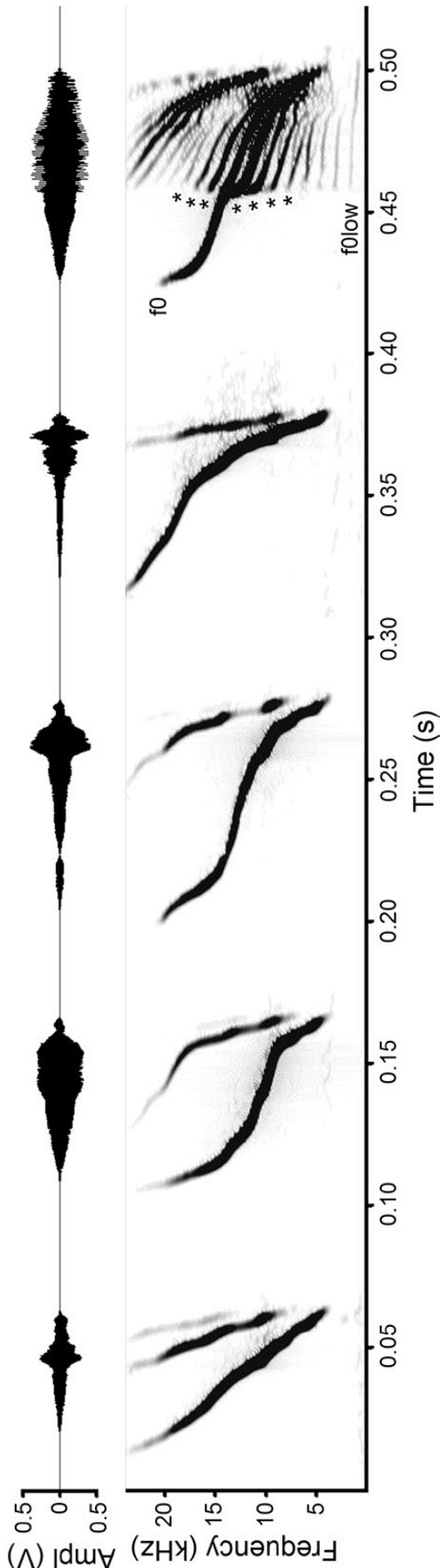
Among the 350 alarm calls analyzed, the fundamental frequency band reached or slightly exceeded the upper limit of the recording equipment (24 kHz) in 78 calls of 16 of the 35 animals, in 1 – 10 (4.9 \pm 3.1) calls per animal for the 16 individuals. Based on the mirror image of the frequencies beyond the limit of the spectrograms, the upper limit was exceeded by no more than 1 – 2 kHz.

This could only slightly affect the f0max of these 78 alarm calls (for all of them, it was measured as 23.9 kHz) but could not affect any other measured acoustic variable (including the

duration and the peak frequency), because all other measurements were made based on the waveform. For example, the maximum values of f0beg did not reach 24 kHz (Table 1). Overall, the actual error of measurements was very small and could not seriously affect the results.

Individual identity of alarm calls.—DFA based on 12 manually measured acoustic variables classified calls to individuals with an accuracy of 93.71%, significantly higher than random (17.28 \pm 1.71%, permutation text, 1,000 permutations, $P < 0.001$). DFA, carried out on the training set of 175 alarm calls, classified calls to individuals with an accuracy of 95.43%. Cross-validating DFA, carried out on the test set of remaining 175 alarm calls using the discriminant functions created for the training set, classified calls to individuals with an accuracy of 86.86% (Table 2). Alarm calls of all 35 animals were classified significantly above chance. Only in two individuals, cross-validating DFA classified 40% alarm calls to correct callers; in all remaining cases correct classification varied between 60% and 100% (Table 2). The first two discriminant functions accounted for only 63.38% of the variation, eight functions had eigenvalues over 1 and, for complete discrimination, 12 discriminant functions were necessary. Wilks' Lambda values revealed that the variables primarily contributing to discrimination included duration, f0mean, and fpeakA (in order of decreasing importance).

DFA based on 12 semiautomatically measured acoustic variables classified alarm calls to individuals with an accuracy of 95.43%, significantly higher than random (17.33 \pm 1.64%, permutation text, 1,000 permutations, $P < 0.001$). DFA, carried out on the training set of 175 alarm calls, classified calls to individuals with an accuracy of 94.29%. Cross-validating DFA, conducted on the test set of remaining 175 alarm calls using discriminant functions created for the training set, classified calls to individuals with an accuracy of 91.43% (Table 2). Only in one individual, cross-validating DFA classified 40%



alarm calls to correct callers; in all remaining cases it varied between 60% and 100% (Table 2). The first two discriminant functions accounted for only 68.51% of variation, nine functions had eigenvalues over 1, and for complete discrimination, 12 discriminant functions were necessary. Wilks' Lambda values revealed that the variables primarily contributing to discrimination included duration, $f0_4$, and $f0_7$ (in order of decreasing importance). Classifying accuracy to individuals did not differ between the two DFAs, based on 12 manually or 12 semiautomatically measured acoustic variables (repeated measures ANOVA, $F_{1,34} = 1.13$, $P = 0.30$).

Despite slightly compromised measurements of $f0_{max}$, we included it in DFA as one of most relevant acoustic variable of the alarm calls of pikas. In DFA, the $f0_{max}$ was not the variable contributing primarily to discrimination. Moreover, the uniform values of $f0_{max}$ in the 78 audible through ultrasonic alarm calls could only decrease the value of correct assignment with DFA but not increase it.

DISCUSSION

Individuality of alarm calls.—We found that alarm calls of Daurian pikas are highly individualized, in spite of their simple contour and the lack of nonlinear phenomena in most individuals. The degree of individualization is comparable to the highly modulated alarm calls of Altai pikas, involving numerous nonlinear phenomena (Volodin et al. 2018). The alarm calls of American pikas and other ground or crevice-dwelling colonial mammals, despite their simple acoustic structure and the lack of nonlinear phenomena, also have a high potential for acoustic discrimination of individuals (Conner 1985a; Matrosova et al. 2009). In Daurian pikas, individuals' alarms may maintain the spatial structure of pika colonies, as has been proposed for Altai pikas (Nikolskii and Mukhamediev 1998; Volodin et al. 2018). Similarly, individual-specific alarm calls were documented by Thompson and Hare (2010) in Richardson's ground squirrels (*Urocitellus richardsonii*), allowing conspecific receivers to distinguish approaching from retreating predators. This suggests that the individually distinctive alarm calls of Daurian pikas may communicate movement of predators among colonies.

These potential functions of individualistic alarms in Daurian pikas are indirectly supported by our observation that alarm calls were produced by colony members practically at each appearance of a surrogate predator (researcher). Most other pika species also are highly vocal toward potential predators (Kawamichi 1969, 1971; Conner 1985a; Lissovsky 2005; Volodin et al. 2018), although some species, such as the Royle's

Fig. 2.—Spectrogram (below) and waveform (above) of the alarm calls (one per individual) of five Daurian pikas. The last alarm call comprises two independent fundamental frequencies: the $f0$ and the $f0_{low}$; asterisks label the combinatorial frequency bands, appearing above and below the fundamental frequency $f0$. The spectrogram was created with a Hamming window, 48 kHz sampling rate, FFT 512 points, frame 50%, and overlap 96.87%. The audio wav-file from which this spectrogram is derived is available as [Supplementary Data SD1](#).

Table 2.—Percent of correct assignment with discriminant function analyses (DFAs) of alarm calls to 35 Daurian pika callers. Three DFAs were based on 12 acoustic variables measured manually and three DFAs were based on 12 acoustic variables measured semiautomatically. DFAs for individuality were conducted on the total set of 350 alarm calls. Training DFAs were conducted on the training set of 175 alarm calls. Cross-validating DFAs were conducted on the test set of remaining 175 alarm calls using discriminant functions created for the training set.

| Animal ID | Variables measured manually | | | Variables measured semiautomatically | | |
|-----------|--|---|---|--|---|---|
| | DFA for individuality (<i>n</i> = 350 calls) | Training DFA (<i>n</i> = 175 calls) | Cross-validating DFA (<i>n</i> = 175 calls) | DFA for individuality (<i>n</i> = 350 calls) | Training DFA (<i>n</i> = 175 calls) | Cross-validating DFA (<i>n</i> = 175 calls) |
| 0502 | 100 | 100 | 100 | 100 | 100 | 100 |
| 0503 | 100 | 100 | 100 | 100 | 100 | 100 |
| 0608 | 100 | 100 | 100 | 100 | 100 | 100 |
| 0616 | 100 | 100 | 100 | 100 | 100 | 100 |
| 0801 | 90 | 100 | 80 | 90 | 100 | 100 |
| 1204 | 100 | 100 | 100 | 100 | 100 | 100 |
| 1209 | 100 | 100 | 60 | 100 | 100 | 100 |
| 1402 | 90 | 80 | 100 | 70 | 80 | 60 |
| 1609 | 90 | 80 | 80 | 90 | 100 | 100 |
| 1610 | 90 | 100 | 100 | 90 | 100 | 80 |
| 1614 | 90 | 100 | 80 | 100 | 80 | 40 |
| 1617 | 100 | 100 | 100 | 100 | 100 | 100 |
| 1619 | 100 | 100 | 100 | 100 | 100 | 100 |
| 1624 | 100 | 100 | 80 | 100 | 100 | 100 |
| 1625 | 100 | 100 | 100 | 100 | 80 | 80 |
| 1626 | 100 | 100 | 100 | 90 | 100 | 80 |
| 1628 | 80 | 60 | 60 | 90 | 80 | 80 |
| 1708 | 80 | 100 | 80 | 90 | 100 | 100 |
| 1709 | 90 | 80 | 40 | 100 | 100 | 100 |
| 1711 | 90 | 80 | 100 | 100 | 100 | 100 |
| 1801 | 80 | 100 | 60 | 100 | 80 | 60 |
| 2001 | 90 | 100 | 80 | 100 | 100 | 100 |
| 2003 | 100 | 100 | 100 | 90 | 100 | 100 |
| 2004 | 90 | 100 | 40 | 90 | 100 | 80 |
| 2005 | 100 | 100 | 100 | 100 | 100 | 80 |
| 2803 | 100 | 100 | 100 | 100 | 100 | 100 |
| 2804 | 80 | 100 | 80 | 90 | 80 | 100 |
| 2805 | 100 | 100 | 100 | 90 | 100 | 80 |
| 3002 | 100 | 100 | 100 | 80 | 60 | 80 |
| 3204 | 80 | 80 | 80 | 100 | 100 | 100 |
| 3308 | 100 | 100 | 100 | 100 | 100 | 100 |
| 3401 | 100 | 100 | 100 | 90 | 80 | 100 |
| 3501 | 100 | 100 | 60 | 100 | 100 | 100 |
| 3503 | 90 | 100 | 100 | 100 | 80 | 100 |
| 3504 | 80 | 80 | 80 | 100 | 100 | 100 |
| Total | 93.71 | 95.43 | 86.86 | 95.43 | 94.29 | 91.43 |

pika, *Ochotona roylei*, only produces alarm calls occasionally (Bhattacharyya et al. 2019). Further research is necessary to investigate whether Daurian pikas can discriminate individuals by their alarm calls.

Further research also is necessary to reveal whether individualistic traits of the alarm calls in Daurian pika are stable within and among years. Whereas male songs and trills of Daurian and Northern pikas retain their individualistic traits among years (Nikolskii et al. 1990; Kojima et al. 2006; Borisova et al. 2013), the alarm call's stability over time has yet to be demonstrated in pikas. In nonhibernating pikas, the individuality of vocal traits probably is more stable over time than in hibernating small ground-dwelling mammals. Limited stability of the individual vocal signature of alarm calls between years was revealed in hibernating ground-dwelling sciurids (*Spermophilus suslicus*—Matrosova et al. 2009, *S. fulvus*—Matrosova et al. 2010a, 2010b, and *S. citellus*—Schneiderová et al. 2017).

High- and low-frequency alarm calls.—Our study confirms earlier findings that Daurian pikas produce the highest-frequency alarm calls among all *Ochotona* species studied to

that effect. The Daurian pika is the first lagomorph species that partly vocalizes in the ultrasonic range. Earlier studies (Nikolskii et al. 1989; Borisova et al. 2008) could not resolve the highest-frequency ultrasonic parts of the Daurian pika alarm calls because the analog cassette recorders used in those studies did not allow recording calls that exceeded 16 kHz.

The production of high- or low-frequency alarm calls by *Ochotona* species does not correlate with body size. In similar-sized Daurian and American pikas, the maximum fundamental frequencies differ up to 15 times: from 16.9 to 23.9 kHz in Daurian pika (Table 1) and from 0.4 to 1.3 kHz in American pika (Somers 1973; Conner 1982). This difference may result from different production modes of the high-frequency and low-frequency alarm calls. The low-frequency alarms might be produced by vibration of the vocal folds in the larynx, as is typical for mammals (Berke and Long 2010). A production mode for the high-frequency alarm calls may be an aerodynamic whistle mechanism, recently confirmed experimentally in certain species of rodents (*Rattus norvegicus*—Riede 2011, 2013; three species of grasshopper mice, *Onychomys*—Pasch et al.

2017). Comparative morphological analyses show that, in the laboratory (Sprague-Dawley strain) Norway rat, *R. norvegicus*, and in the northern pygmy mouse, *Baiomys taylori*, the production of high-frequency calls is supported by the presence of a ventral pouch and alar cartilage (Riede et al. 2017; Riede and Pasch 2020). Further morphological study is necessary to reveal whether comparable anatomical structures also are present in the Daurian pika.

An additional argument in support of the whistling production mechanism for the Daurian pika alarm call is the finding of two independent fundamental frequencies in all alarm calls of one Daurian pika individual. Two independent and mutually interacting fundamental frequencies within the same call certainly are produced by two different sound sources (Wilden et al. 1998). The production mechanism for the high fundamental frequency (20.41 – 4.08 kHz) of the biphonic call might be an aerodynamic whistle. The production mechanism for the low fundamental frequency (1.64 – 0.82 kHz) of the biphonic call might be vibrations of the vocal folds, because it matches the value of the fundamental frequency of 0.4 – 1.3 kHz observed in the alarm calls of American pikas (Somers 1973; Conner 1982).

The distributional range of Daurian pika is within the geographic area representing the evolutionary center of the origin of lagomorphs (Ge et al. 2013). Whistling possibly may represent the ancestral default-mode of alarm call production in pikas, whereas the low-frequency alarms of the American pikas are an evolutionary novelty. An alternative evolutionary scenario is that ancestral pikas produced calls with two (high and low) fundamental frequencies, as did the individual with nonlinear phenomena in our study. During dispersal to North America, American pikas retained only the low fundamental variant, whereas the Asian pikas mostly retained the high one. This situation is reminiscent of the evolution of male rutting calls during the radiation of red deer, *Cervus elaphus*, and dispersal from their center of origin in Central Asia (Frey and Riede 2013; Volodin et al. 2013). Recent red deer living in that center of origin retained male rutting calls with two (high and low) fundamental frequencies, whereas two lineages dispersing to the West or East of the center of origin, retained only one of the two fundamental frequencies, either the low or the high one (Volodin et al. 2013). The selection pressure for the evolutionary reduction of certain call components in radiated lineages of pikas and red deer remains to be identified.

In a third evolutionary scenario, ancestral pikas produced only low-frequency alarm calls because vocal fold vibration is the default-mode of vocalization in mammals. As a consequence, American pikas would have retained the ancestral low-frequency alarm calls, whereas the Asian stock evolved novel, potentially more efficient, high-frequency alarm calls involving a different mechanism of call production (Titze and Palaparathi 2018), and a novel protective outer ear mechanism (Lisovsky 2005; Volodin et al. 2018).

In Daurian pikas, we could occasionally observe and videotape outer ear-folding and depression synchronous with the emission of their intense alarm calls. These video data, as well

as the anatomical background of this behavior, have yet to be analyzed. Very intense alarm calls, as well as call-synchronized outer ear-folding and depression as a behavior potentially protecting the middle and inner ear from damage by self-generated calls, also were reported for Altai pikas (Lisovsky 2005; Volodin et al. 2018) and Northern pikas (Lisovsky 2005). In contrast, no such call-synchronized movements of the pinna were observed in American pikas, which produce low-frequency alarm calls below 1.5 kHz (Somers 1973; Conner 1982; Titze and Palaparathi 2018) or in Royle's pikas, *O. roylei*, which produce only faint calls hardly noticeable at distances greater than a few meters (Kawamichi 1968; Bhattacharyya et al. 2019). Possibly, selection pressures for evolving a protective outer ear mechanism arose from the higher radiation power of high-frequency calls compared to low-frequency calls of the same intensity (Titze and Palaparathi 2018).

Alarm calls as long-range signals.—Producing calls with a contour covering a wide range of frequencies, as in the alarm calls of Daurian pikas, potentially increases caller localizability. Low frequencies propagate omnidirectionally, the higher frequencies of the same call will propagate with a more narrow beam (Frommolt and Gebler 2004). For conspecifics, this difference in propagation of the higher- and lower-frequency call parts might provide acoustic cues to caller orientation toward a receiver (Miller 2002; Sloan et al. 2005; Volodin et al. 2006; Volodina et al. 2006).

Alarm calls produced at high intensity with an open mouth and a special vocal posture, as in pikas, can propagate over a relatively long distance to be heard by members of neighboring colonies (Titze and Palaparathi 2018; Volodin et al. 2018). Although we did not measure the alarm call intensity in Daurian pikas in this study, the calls could be heard from a distance of about 30 – 50 m, despite the limited abilities of adult humans to hear frequencies above 15 kHz (Masterton et al. 1969). Although hearing range has not been investigated in pikas, the hearing sensitivity range of another lagomorph, the domestic rabbit *Oryctolagus cuniculus* ranges from 0.2 to 32 kHz (Heffner and Masterton 1980). It encompasses the entire frequency range of pika alarm calls, from 0.4 kHz, as in the lowest alarms of American pikas (Somers 1973; Conner 1982) up to 23.9 kHz, representing the upper frequency limit in the alarm calls of Daurian pikas established in this study.

Manual and semiautomatic acoustic measurements.—Comparison of the measurement of acoustic variables using the manual versus semiautomatic method did not reveal any distinct advantage of either method. Both approaches provided similar results for estimating the degree of individuality in the alarm calls of Daurian pikas with DFA. However, the semiautomatic method is less time-consuming. We recommend it for the rapid measurement of calls with simple acoustic structure and with a relatively high fundamental frequency, such that any background noise can be filtered out easily. When using the semiautomatic approach, it is necessary to visualize the peak frequency and check whether it matches the fundamental frequency by superposition on the spectrogram.

Audible through ultrasonic alarm calls.—Our study demonstrates that the maximum fundamental frequency of alarm calls of Daurian pikas is substantially higher than the 16 kHz previously reported by [Nikolskii et al. \(1989\)](#), and that f_{0max} of some calls can exceed 24 kHz. We suggest that recorders with a sampling rate of up to 96 kHz and microphones with a flat response from 2–3 to 40–50 kHz be used to further investigate the alarm calls of Daurian pikas. This suggestion also applies to recording alarm calls of the Northern pika *O. hyperborea*, because some populations of this species produce high-frequency alarm calls with a descending contour shape, reminiscent of those in Daurian pika ([Lissovsky 2005](#)).

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Alarm calls (one per individual) of five Daurian pikas.

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