EFFECTS OF WIND ON THE BEHAVIOR AND CALL TRANSMISSION OF PIKAS (*OCHOTONA PRINCEPS*)

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It has been suggested that pikas are less active during inclement weather. We hypothesized that this decrease in activity is a predator-avoidance response to wind conditions that decrease the effectiveness of the alarm calls of pikas. We examined this hypothesis by broadcasting and rerecording the prominent frequencies (900–5,500 Hz) of pikas' calls and by observing behavior of focal pikas during varying weather conditions. Both attenuation of pure tones and the amount of wind noise increased significantly as wind speed increased. Additionally, wind direction created asymmetrical patterns of attenuation of pure tones, potentially distorting and degrading the call. Further, pikas spent significantly more time inactive at higher wind speeds, with nonvigilant active behaviors decreasing at a higher rate than vigilant active behaviors. Examination of these data supports the hypothesis and suggests that wind influences the behavior of animals that rely on alarm calls.

Key words: alarm call, behavior, noise, *Ochotona princeps*, pika, predator avoidance, vigilance, weather, wind

It is assumed that alarm calls provide antipredator benefit and that they function best when they are detected accurately by the intended receiver or receivers (Hobbs 1980). It might then be expected that weather conditions that impede effective transfer of alarm calls would create risky situations, and that ability to respond to the factors that impede call transfer would enable animals to reduce increased risk. Wind is one such condition and could diminish alarm call effectiveness by increasing attenuation and degradation of the call and by increasing background noise that could compete with the call (Daniel and Blumstein 1998; Langemann et al. 1998; Larom et al. 1997; Morton 1975; Richards and Wiley 1980; Ryan and Brenowitz 1985; Wiley and Richards 1982).

Under ideal acoustic conditions (homogeneous, frictionless environment), sound pressure levels decrease at a rate of $1/r^2$ because of the inverse square law, where r is the distance between source and receiver. In natural environments, excess attenuation (loss of amplitude at a rate greater than expected from the inverse square law) can result from absorption and scattering by turbulent air (Kime et al. 2000; Naguib et al. 2000; Wiley and Richards 1982) and thus can reduce the distance at which sounds can be detected.

Further, simple detection of an alarm call may not be sufficient, if essential information is present in the structure of a signal. Degradation of the signal, as a result of differential attenuation of tone frequencies (frequency-dependent attenuation) caused by factors including atmospheric turbulence, can reduce the information available to the recipient of the signal (Daniel and Blumstein 1998; Naguib et al. 2000; Richards and Wiley 1980; Wiley and Richards 1982).

Noise is any sound that interferes with effective transmission of a signal and may be physical (e.g., wind and precipitation) or biological (e.g., communication by other species—Forrest 1994) in origin. High ambient noise may mask a signal by reducing the signal-to-noise ratio below the critical level necessary for detection and discrimination (Kime et al. 2000; Langemann et al. 1998).

The American pika (*Ochotona princeps*) is a diurnally active and easily observable inhabitant of talus or other rock piles in alpine and subalpine environments, which are prone to weather fluctuations over relatively short time periods. These small (100- to 150-g) herbivores occupy individual territories that typically range from 400 to more than 4,500 m^2 (Barash 1973; Lutton 1975). Potential predators of pikas include *Canis latrans*, *Mustela frenata*, *Mustela erminea*, *Martes americana*, and large birds (Lutton 1975; Smith and Weston 1990). Because pikas cannot physically defend themselves when attacked, their primary means of avoiding predation is to seek refuge within the interstices of the talus (McKechnie et al. 1994). The signal initiating the impetus to flee to safety may be direct detection of the predator or the alarm call of a conspecific.

The alarm vocalizations of pikas are referred to as "short calls" and consist of 1 or occasionally 2 notes, each with abundant harmonics (Somers 1973). Short calls vary geographically, although notes typically last 0.15–0.45 s with frequencies ranging from 400 to 8,000 Hz (Conner 1982; Somers 1973).
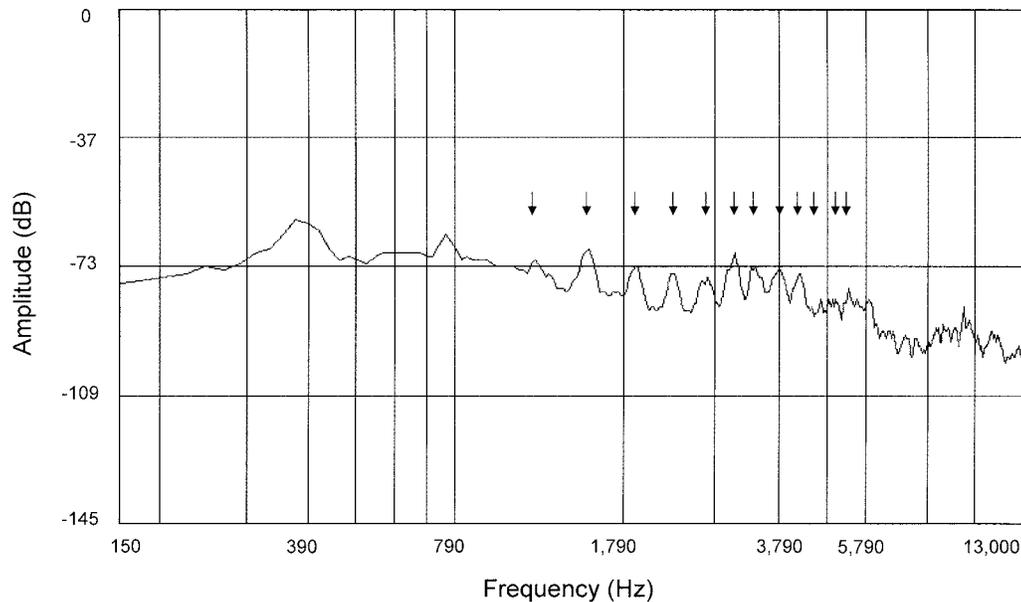
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Fɪɢ. 1.—Spectrogram of the pika short call obtained from the Macaulay Library of Natural Sounds at Cornell University and used to identify prominent frequencies, indicated by arrows at 900, 1,400, 1,800, 2,200, 2,700, 3,100, 3,500, 3,900, 4,300, 4,700, 5,100, and 5,500 Hz, that were broadcast as pure tones and rerecorded under various weather conditions.

These calls are commonly emitted in a series, often after a predator has left a pika's immediate vicinity (Ivins and Smith 1983). Pikas typically respond to these calls by pausing and looking in the direction of the caller before fleeing into the rocks or resuming previous activity (Conner 1982; Somers 1973).

Several investigators have noted that pikas seem to spend more time inactive within the talus when weather is inclement (Barash 1973; Orr 1977). It is unlikely that such a reduction in activity would be related to conservation of heat. Pikas are cold-adapted and their dense pelage limits dissipation of metabolic heat and may cause hyperthermia and death after short periods of exposure to moderate (25.5–29.4°C) ambient temperatures (MacArthur and Wang 1973, 1974; Smith 1974; Smith and Weston 1990); thus, wind-induced cooling would be expected to be of thermal advantage to pikas. We hypothesized that pikas increase time spent hidden within the talus when environmental conditions decrease the protection provided by the effective transfer of alarm calls and that this behavior reduces exposure to predators.

To evaluate this hypothesis, we observed pikas and evaluated the effect of wind-induced noise and acoustic disturbance to determine if short-term variations in weather affect call transmission and produce predictable patterns of pika behavior. We predicted that, as wind speed increases, attenuation and degradation of calls and competition with background noise all would increase; and the time that pikas spend inactive would increase, with nonvigilant behaviors decreasing at a higher rate than vigilant behaviors.

MATERIALS AND METHODS

Study site.—We conducted research in the Sawtooth Mountains of central Idaho during the summer of 2001. The study site was talus with a slope of about 45°, located at about 2,300 m elevation and about 30 km west of Stanley, Idaho, and to the south of Cape Horn Creek, near Forest Road 579 in the Challis National Forest. The subalpine area consisted primarily of talus slide interspersed with large areas of vegetation and fallen trees. The habitat was bordered by coniferous forest to the east and west, a small riparian area along the base of the slide, and granite cliffs at the top of the slope.

Animal handling.—We captured pikas by using apple-baited live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) that were checked hourly. We placed captured pikas in a clear, plastic enclosure and delivered a cotton ball containing a dose of anesthetic isoflurane gas (Halocarbon Laboratories, River Edge, New Jersey) before ear tagging. We inserted unique color combinations of rabbit ear tags (National Band and Tag Company, Newport, Kentucky) in holes created with a punch (National Band and Tag Company). All trapping and ear-tagging procedures followed guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by the Animal Welfare Committeee of Idaho State University.

Weather data.—We recorded the maximum wind speed and maximum temperature during each sound recording or observation period by using a Skywatch Elite omnidirectional anemometer (Speedtech Instruments, Great Falls, Virginia). Conditions below the threshold necessary for the anemometer to register a wind speed value were recorded as "no wind." We recorded intensity of visible light by using an LI-170 photometer (Li-Cor, Lincoln, Nebraska), and we estimated wind direction from the movement of vinyl flags. We positioned each weather instrument and flag about 20 cm from the rock surface to sample the same microenvironment in which alarm calls were transmitted and received.

Sound recordings.—We assumed that factors that influence individual sound frequencies would likely affect complete pika calls. Thus, we determined the influence of weather variables on the transmission of sound through a pika's environment by using a range of pure tones, selected from frequencies of short calls of a pika, which we broadcast and rerecorded during different weather conditions. We acquired a recording of 2 pika short calls from the Macaulay Library of Natural Sounds at Cornell University and analyzed them by using JBL Smaart Pro (SIA Software Company, Whitinsville, Massachusetts) to determine prominent frequencies of the calls (Fig. 1). We

selected 12 frequencies (900; 1,400; 1,800; 2,200; 2,700; 3,100; 3,500; 3,900; 4,300; 4,700; 5,100; and 5,500 Hz); there were also amplitude peaks at 375 and 775 Hz, but we believe these were noise that is not associated with the pika call. We recorded pure tones of these frequencies on a compact disc by using Sound Forge 5.0 (Sonic Foundry, Madison, Wisconsin). Each pure tone was recorded for a 5-s interval with 2 s of silence between adjacent pure tones.

We broadcast and rerecorded these tones at 3 locations near the territories of focal pikas. At each location, we broadcast the pure tones by using a Sony ZS-X7 personal audio system (Sony Corporation, Tokyo, Japan) that we rotated to face into (against), with, and perpendicular to the prevailing wind direction. The audio system was situated ~10 cm from the surface of the rock, approximating the height at which pikas commonly emit their calls. The speaker had a relatively flat response within the range of frequencies that we used and we set the amplitude at a constant level to provide the maximum signal output that could be produced without creating distortion.

We rerecorded the transmitted tones at distances of 1, 10, and 25 m onto Sony PDP-95C digital audiotapes (Sony Corporation) with a cardioid Audio-Technica MB2000L dynamic microphone (Audio-Technica, Stow, Ohio) connected to a Sony PCM-M1 digital audio recorder (Sony Corporation). The calls of pikas are commonly heard at distances greater than 25 m, but this maximum distance insured adequate signal-to-noise ratios for analysis. It was assumed that the polar pattern of a cardioid microphone best simulates the directional hearing that is likely found in pikas, based on the common tendency of pikas to shift the focus of their cup-shaped ears. We kept the recording level constant for all treatments and directed the microphone toward the speaker at a height of ~10 cm above the surface, corresponding roughly to the height of a pika's ears.

Sound analysis.—We imported the recorded data into Sound Forge 5.0 as wave files and normalized each file to obtain maximum unclipped sound levels for analysis. We measured relative sound pressure levels of each recorded pure tone by using the spectrum analysis function. We calculated excess attenuation by subtracting the measured sound pressure levels at 10- and 25-m distances from those recorded at a 1-m distance for each pure tone frequency and then determined the difference between these values and those calculated by using the inverse square law. Because frequencies at which pikas transmit information are unknown, we examined both the average of the excess attenuation values calculated for all pure tone frequencies combined (average excess attenuation) and the separate excess attenuation values for each individual pure tone frequency (discrete frequency-dependent excess attenuation). We examined degradation by determining if excess attenuation differed among pure tone frequencies, which would indicate differential change in effectiveness of transmission across the frequencies comprising an alarm call. We measured the wind noise found within the 2-s intervals between pure tones by using the spectrum analysis function to calculate relative sound pressure levels of frequencies ranging from 50 to 5,500 Hz and at 5 levels of wind speed: no wind, >0–2 m/s (average 1.3 m/s), >2–3 m/s (average 2.5 m/s), >3–4 m/s (average 3.1 m/s), and ≥5 m/s (average 5.4 m/s).

Behavioral observations.—We estimated frequency and duration of behaviors of 6 focal animals (Altmann 1974), including 3 male and 3 female pikas with adjacent, clumped, and dispersed territories. We determined territories by observing the range that each pika traveled from its haypile, and we established permanent observation points at locations that provided a view of the majority of each pika's territory. Upon arriving at a pika's territory, the observer was inactive for 10 min to allow pikas to acclimate to the observer's presence and to provide the observer time to locate the focal individual. If pikas

TABLE 1.—Multiple linear regression of average excess attenuation (dB) with wind speed, distance, and wind directions measured in pika habitat in Idaho (model $r^2 = 0.253$, $F = 3.388$, *d.f.* = 5, 50, $P = 0.010$).

Variable	Coefficient	*SE*	*F*	*P*
Constant	3.996	3.478	1.320	0.256
Wind speed	1.548	0.876	2.650	0.084
Distance	0.245	0.150	3.119	0.110
Wind direction	—	—	2.546	0.066
With wind	−3.638	3.421	1.130	0.293
Into wind	5.051	3.639	1.927	0.171
Perpendicular to wind	2.062	3.582	0.332	0.567

are allowed a brief acclimation period, they do not respond to the presence of human observers (Holmes 1991; Huntly et al. 1986; Ivins and Smith 1983; Roach et al. 2001).

We observed each focal pika for 6 consecutive 5-min periods and recorded each behavior and the length of time that it persisted. Behaviors were classified as grazing (eats plant material as it is gathered), grooming (cleans itself), haying (gathers plant, fecal, or animal material and immediately returns to the haypile with the material), inactive (disappears from the sight of the viewer), perching (perches upon a rock, or other viewing point, as a separate activity), running (moves from place to place within the habitat), scanning (stops another activity, momentarily, to look around), and short call (emits a single, or a series of single, call notes). Weather variables were measured throughout each observation and recorded at the end of each 5-min period. We made observations between 25 July and 14 September 2001, between 0700 and 2100 h.

Statistical analyses.—We used multiple linear regression to detect correlations of average excess attenuation with wind speed, distance from the speaker, and direction of wind relative to the broadcast (coded by using indicator variables with ''no wind'' as the reference class and entered as a block).

Each sound recording included all pure tone frequencies and was associated with a single measure of weather variables. Therefore, we tested the effect of wind speed, distance, wind direction, and pure tone frequency on excess attenuation and degradation with repeated-measures analysis of variance, which effectively treated each full set of frequencies as a block. We entered distance and wind speed as continuous variables and wind direction and pure tone frequency as categorical variables.

We tested the effect of wind speed and pure tone frequency on wind noise by using multiple linear regression, by using a natural logarithm transformation of frequency (ln frequency) to linearize the pure tone frequency data. Wind speed was coded as indicator variables that grouped recordings taken at similar wind speeds into 5 categories: no wind, >0–2 m/s, >2–3 m/s, >3–4 m/s, and ≥5 m/s (''no wind'' was used as the reference class).

We used multiple linear regression to detect correlations between time spent inactive and weather variables and logistic regression to detect correlations between weather variables and the activities of pikas. To determine if wind could predict time that pikas spent inactive, after other potential influences on behavior were accounted for, we added temperature, light, time (hour of day), and time^2 (to examine crepuscular behavior, which is a nonlinear [hyperbolic] function of time) to the model. We coded each focal pika and focal pika × weather variable interaction as an indicator variable and entered each as a block to account for the lack of independence of repeated observations of each pika. We used backward stepwise regression to obtain
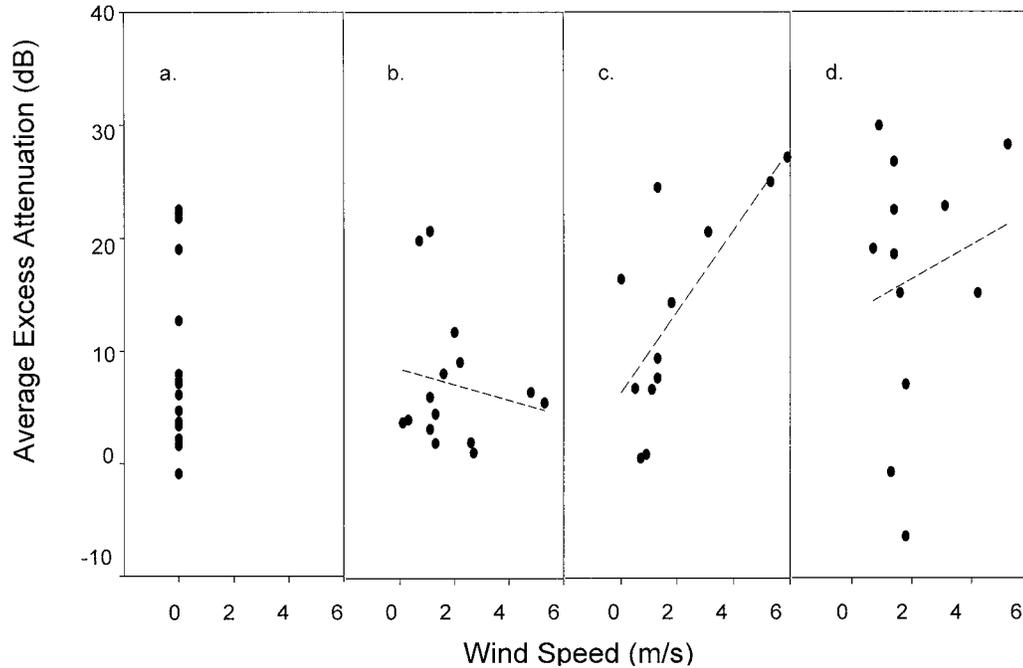
FIG. 2.—Average excess attenuation of the prominent frequencies of a pika call as a function of wind speed and wind direction measured in Idaho. Pure tones were broadcast in conditions of a) no wind, b) in the direction of the wind, c) into the wind, and d) perpendicular to the wind. Average excess attenuation increased with increasing wind speeds ($P < 0.09$) and was also influenced by wind direction ($P < 0.07$).

the best model describing the influence of weather variables on time spent inactive, with $P > 0.05$ as the criterion for removal. Similarly, we used backward stepwise logistic regression to test whether speed of wind predicted activities of pikas, with behaviors coded as categorical presence or absence variables, and with $P > 0.05$ as the criterion for removal. All statistical procedures were conducted by using SPSS for Windows version 11 software (SPSS Inc., Chicago, Illinois).

RESULTS

We made 56 sets of recordings (3 distances × 12 frequencies) that included 19 with no wind, 13 measured in the direction of the wind, 12 into the wind, and 12 perpendicular to the wind. Wind speed during the recordings

TABLE 2.—Repeated-measures analysis of variance for discrete excess attenuation values (dB) measured in pika habitat in Idaho with wind direction, distance, wind speed, pure tone frequency, and the interaction of wind direction, distance, and wind speed with pure tone frequency.[a]

Source of variation	d.f.	SS	MS	F	P
Between subjects					
Wind direction	3	7,953.088	2,651.029	3.306	0.028
Distance	1	2,490.505	2,490.505	3.106	0.084
Wind speed	1	3,764.827	3,764.827	4.695	0.035
Within subjects					
Pure tone frequency	11	186.147	16.922	0.416	0.949
Pure tone frequency × direction	33	5,414.784	164.084	4.032	0.000
Pure tone frequency × distance	11	352.229	32.021	0.787	0.654
Pure tone frequency × speed	11	721.634	65.603	1.612	0.092

[a] SS = sum of squares; MS = mean squares.

ranged from 0 to 5.9 m/s (average 1.3 m/s). We also recorded 417 five-min observations of the 6 adult pikas, with number of observation periods per pika ranging from 65 to 72. Pikas were scored as inactive during 97.8% of observation periods, perching 42.7%, haying 38.1%, running 37.4%, scanning 37.4%, short calling 35.5%, grooming 24.9%, and grazing 19.9%. Wind speeds during observations were 0–6.5 m/s (average 1.2 m/s), temperature was 5–39°C (average 22°C), and light intensity was 4–2, 400 W/m^2 (average 602.5 W/m^2).

Sound recordings.—Average excess attenuation and discrete frequency-dependent excess attenuation of call tones were influenced by wind speed and direction. Overall, average excess attenuation increased with increasing wind speeds, and attenuation was least when calls were emitted in the direction of the wind and greatest when calls were directed into the wind (Table 1; Fig. 2). Frequency-dependent attenuation increased significantly with increasing wind speed ($P < 0.04$), and this response varied significantly with wind direction ($P < 0.03$; Table 2). There was little relationship between distance from the speaker and average excess attenuation.

Degradation of the rerecorded pure tones varied significantly with wind direction ($P < 0.001$; Table 2). High pure tone frequencies in particular were more attenuated when tones were broadcast against and perpendicular to the wind than when they were broadcast in conditions of no wind or in the direction of the wind (Fig. 3).

Additionally, wind noise was significantly related to wind speed and frequency (Table 3), increasing with wind speed, but only detectable at frequencies <500 Hz (Fig. 4). The significant interaction between wind speed and ln frequency
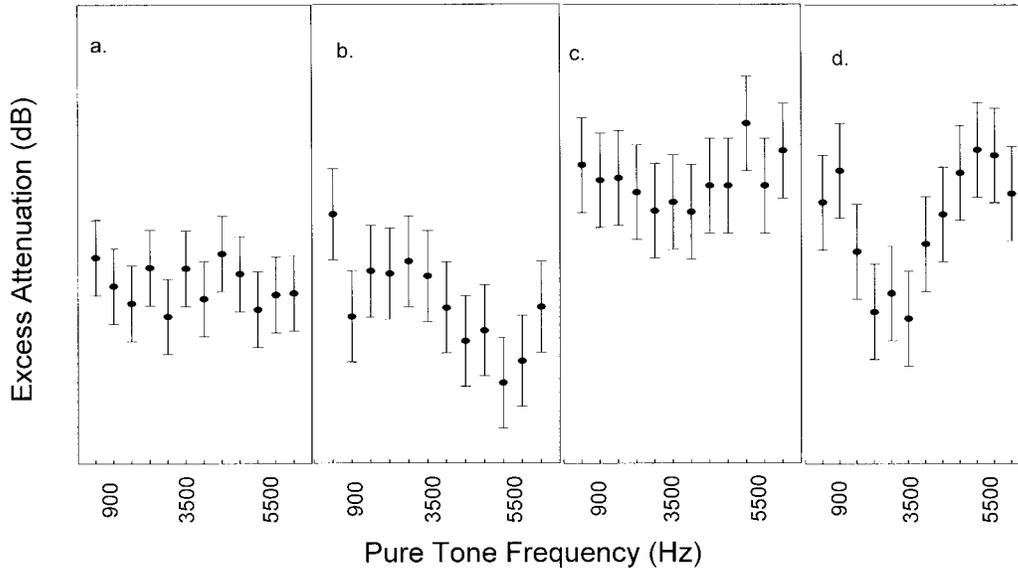
Fig. 3.—Excess attenuation ($\bar{X} \pm 1$ *SE*) of the prominent frequencies of a pika call as a function of pure tone frequency and wind direction measured. Pure tones were broadcast in pika habitat in Idaho in conditions of a) no wind, b) in direction of the wind, c) into the wind, and d) perpendicular to the wind. Higher-frequency pure tones were more attenuated when directed into and perpendicular to the wind than when directed in conditions of no wind or in the direction of the wind ($P < 0.001$).

reflected increased noise at higher frequencies and higher wind speeds. Both effects of wind speed and of the interaction of wind speed with frequency were larger at greater wind speeds and were highly significant at wind speeds greater than 2 m/s (Table 3).

Behavioral observations.—The amount of time that pikas were inactive was strongly influenced by weather (Table 4). Time inactive increased particularly strongly with wind speed, 21.78 s for each 1 m/s, and complete inactivity occurred when wind speeds exceeded 4 m/s. Time inactive also increased an average of 3.59 s with each 1°C increase in temperature and decreased by 0.04 s with each increase of 1 W/m² in light intensity. Pikas were less active in the middle of the day, and this pattern was hyperbolic, reflecting crepuscular activity.

Each of the active behaviors of pikas also was influenced by weather. Grazing, grooming, haying, perching, running, scanning, and short calling all decreased significantly with wind speed (Table 5). The probability of grazing decreased by 31.6%, perching by 34.6%, grooming by 37%, calling by 38.3%, running by 46.2%, scanning by 54%, and haying by 56.7% for each 1-m/s increase in wind speed. The only significant changes in behavior associated with increasing temperature were decreases in activity; running decreased 5.2%, scanning 7.3%, haying 7.5%, and perching 18.2% for each 1°C increase in temperature. Grooming, haying, scanning, and calling showed crepuscular patterns, with less activity during the middle of the day. Also, individual pikas differed in their levels of response to weather, as indicated by significant effects of pika and pika × weather variable blocks.

DISCUSSION

Results of this study supported our hypothesis that wind interferes with alarm calls of pikas and that pikas are less likely to engage in active behaviors, especially nonvigilant behaviors, during windy conditions. The effects of wind on behavior were significant and were independent of effects of weather-associated changes in temperature and light.

Both wind speed and wind direction caused attenuation of alarm calls. Excess attenuation increased with wind speed, and wind direction affected the symmetry of signal transmission. Pure tones had the least attenuation when transmitted in the direction of the wind and the most attenuation when directed into the wind (Table 1). This asymmetrical transmission of pure tone frequencies likely decreases the stability of communication and increases predation risk.

Wind direction caused differential attenuation of pure tone frequencies, indicating that windy conditions degrade alarm calls of pikas. As expected (Smith 1979), high-frequency pure tones were significantly more attenuated than lower-frequency

TABLE 3.—Multiple linear regression of wind noise (dB) measured in pika habitat in Idaho with ln frequency, wind speed indicator variables, and interaction of wind speed indicator variables with ln frequency (model r² = 0.740, F = 87.013, *d.f.* = 4, 275, *P* < 0.001).

| Variable	Coefficient	*SE*	*T*	*P*
Constant	−36.368	6.174	−5.890	0.000
ln Frequency	−8.099	0.952	−8.506	0.000
Wind speed > 0−2 m/s	7.719	8.732	0.884	0.377
Wind speed > 2−3 m/s	28.928	8.732	3.313	0.001
Wind speed > 3−4 m/s	35.707	9.432	3.786	0.000
Wind speed ≥ 5 m/s	57.501	8.732	6.585	0.000
ln Frequency × wind speed > 0−2 m/s	0.005	1.347	0.004	0.997
ln Frequency × wind speed > 2−3 m/s	−2.963	1.347	−2.201	0.029
ln Frequency × wind speed > 3−4 m/s	−3.470	1.454	−2.386	0.018
ln Frequency × wind speed ≥ 5 m/s	−6.028	1.347	−4.476	0.000
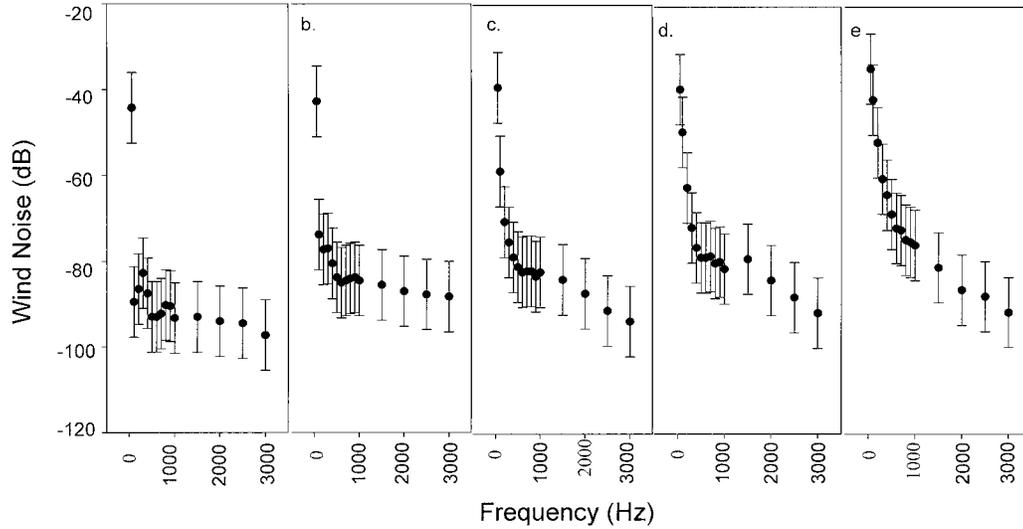
FIG. 4.—Wind-generated noise levels ($\bar{X} \pm 1$ SE) as a function of wind speed and frequency. Recordings were taken in pika habitat in Idaho in conditions of a) no wind, b) >0–2 m/s, c) >2–3 m/s, d) >3–4 m/s, and e) ≥5 m/s. Wind noise increased with increasing wind speeds ($P < 0.05$) but was found only at frequencies < 500 Hz.

pure tones when broadcast into or perpendicular to the wind (Fig. 3). This likely reflects the lower energy and smaller wave size of higher-frequency tones, which would make them more susceptible to scattering from atmospheric turbulence. Increased degradation of high-frequency components of calls during windy conditions may limit the ability of pikas to discriminate information at those frequencies.

Wind-generated noise also increased with wind speeds, was less at higher frequencies, and was primarily found at frequencies lower than 500 Hz (Fig. 4). Although examination of our data showed wind noise primarily at frequencies below those that are prominent in the alarm calls of pikas, this likely reflected the relatively low wind speeds during the study. Noise at higher frequencies, caused by higher wind speeds, might mask the lower frequency components of alarm calls, making them more difficult to detect.

This is the 1st study to quantify the anecdotal observation that pikas spend more time vigilant and inactive within the talus when weather is inclement. The behavior of pikas has been shown to be sensitive to risk, and risk of predation increases when pikas are active aboveground (Holmes 1991; Ivins and Smith 1983; Lutton 1975). Pikas spent significantly

TABLE 4.—Final model obtained from backward stepwise linear regression of time pikas spent inactive in Idaho during 5-min observations (model $r^2 = 0.372$, $F = 15.818$, $d.f. = 15$, 401, $P < 0.001$).

Variable	Coefficient	SE	F	P
Wind speed	21.776	4.301	25.634	0.000
Temperature	3.588	0.930	14.891	0.000
Light	−0.041	0.012	12.623	0.000
Time	37.417	13.546	7.629	0.006
Time^2	−1.511	0.491	9.462	0.002
Pika	—	—	3.206	0.008
Pika × light	—	—	5.092	0.000
Constant	−93.825	76.743	1.495	0.222

more time inactive as wind speed increased, and they spent the entire observation period inactive when wind speeds exceeded 4 m/s, consistent with the prediction that pikas reduce risk of predation by reducing their exposure to predators during windy conditions when their alarm calls are less effective.

The pattern of relative decrease of behaviors as wind speed increased further suggests that the decreased activity by pikas is a response to predation risk. Haying, running, and scanning were the behaviors most sensitive to wind. Haying, which typically occurs away from the cover of talus, and running are both behaviors that involve exposure to predators and would be expected to decrease during risky time periods, and scanning, by definition, is vigilance during active movement, so declines when haying or running decline. Perching, calling, and grazing were least sensitive to wind, but perching and calling are vigilant behaviors and so might be retained as part of any activity. The relatively low sensitivity of grazing to high wind speeds may reflect the inability of pikas to interrupt their food intake for long because of their high metabolic rate (Smith and Weston 1990).

Both the excess attenuation of pure tones and the amount of wind noise increased with wind speed, and wind direction created asymmetrical call transmission patterns, degrading the structure of the overall call. Even at the relatively low levels of wind encountered during this study, pika spent less time active as wind speeds increased, indicating strong sensitivity to wind. These results are consistent with the hypothesis that decreased activity is a predator-avoidance response to conditions that decrease the protection provided by effective transfer of alarm calls. Previous studies of predator avoidance have shown that proximity to safety (Holmes 1984, 1991; Schneider 1984), predator activity (Caldwell 1986), energetic status (Hilton et al. 1999), light intensity, cloud cover, precipitation (Hilton et al. 1999; Kotler 1984; Lima 1988a, 1988b), and group size (Roberts 1996; Treves 2000; White et al. 2001) influence risk of predation and behavior of prey, but the influence of wind has been

TABLE 5.—Final model obtained from backward stepwise logistic regressions of pika behaviors in Idaho during 5-min observation period on variables and interactions shown. Table entries are model coefficients and associated P values: B for single factors and Wald for multiple d.f. blocks.

Factor (d.f.)	Calling	Calling P	Grazing	Grazing P	Grooming	Grooming P	Haying	Haying P	Perching	Perching P	Running	Running P	Scanning	Scanning P
Constant (1)	4.487	0.025	−1.082	0.000	8.081	0.030	7.31	0.006	−1.162	0.688	9.38	0.001	12.053	0.000
Wind (1)	−0.483	0.000	−0.38	0.001	−0.463	0.057	−0.838	0.001	−0.425	0.014	−0.62	0.000	−0.777	0.000
Temperature (1)	—	—	—	—	—	—	−0.077	0.006	—	—	−0.053	0.032	−0.076	0.014
Light (1)	—	—	—	—	—	—	—	—	—	—	−1.162	0.017	0.001	0.029
Time (1)	−0.876	0.015	—	—	−1.507	0.017	−1.036	0.030	—	—	0.044	0.013	−1.684	0.001
Time^2 (1)	0.034	0.011	—	—	0.056	0.014	0.042	0.015	—	—	—	—	0.066	0.000
Pika (5)	—	—	13.249	0.021	14.249	0.014	24.215	0.001	3.207	0.019	15.386	0.009	23.952	0.000
Pika × wind (5)	—	—	—	—	15.130	0.010	16.73	0.005	—	—	25.406	0.000	18.594	0.002
Pika × temperature (5)	—	—	—	—	—	—	—	—	11.163	0.048	—	—	—	—
Pika × light (5)	—	—	—	—	—	—	—	—	11.367	0.045	—	—	—	—
Pika × time (5)	—	—	—	—	14.138	0.015	—	—	16.198	0.006	—	—	—	—
Pika × time^2 (5)	18.101	0.003	—	—	13.230	0.030	20.31	0.006	15.938	0.007	—	—	—	—
Model χ^2 (d.f.)	93.933 (13)		27.359 (6)		82.64 (23)		179.27 (19)		147.979 (30)		166.229 (14)		191.701 (15)	
Model n	418		418		418		418		418		418		418	
Model P	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001	

relatively unappreciated. Our study indicates that wind may substantially decrease the effectiveness of alarm calls, resulting in behavioral avoidance of exposure to predators, which may compensate for decreased protection through alarm calls. Because similar decreases in call effectiveness are likely to be widespread, future studies should consider the impact of wind on the behavior of other species that rely on alarm call vocalizations.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

BARASH, D. P. 1973. Territorial and foraging behavior of pika (Ochotona princeps) in Montana. American Midland Naturalist 89:202–207.

CALDWELL, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. Auk 103:494–505.

CONNER, D. A. 1982. Geographic variation in short calls of pikas (Ochotona princeps). Journal of Mammalogy 63:48–52.

DANIEL, J. C., AND D. T. BLUMSTEIN. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour 56:1517–1528.

FORREST, T. G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. American Zoologist 34:644–654.

HILTON, G. M., G. D. RUXTON, AND W. CRESSWELL. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. Oikos 87:295–302.

HOBBS, D. E. 1980. The effect of habitat sound properties on alarm calling behavior in two species of tree squirrels (Sciurus nayaritensis and Sciurus arizonensis). Ph.D. dissertation, University of Arizona, Tucson.

HOLMES, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. Behavioral Ecology and Sociobiology 15:293–301.

HOLMES, W. G. 1991. Predator risk affects foraging behavior of pikas: observational and experimental evidence. Animal Behaviour 42:111–119.

HUNTLY, N. J., A. T. SMITH, AND B. L. IVINS. 1986. Foraging behavior of the pika (Ochotona princeps), with comparisons of grazing versus haying. Journal of Mammalogy 67:139–148.

IVINS, B. L., AND A. T. SMITH. 1983. Responses of pikas (Ochotona princeps, Lagomorpha) to naturally occurring terrestrial predators. Behavioral Ecology and Sociobiology 13:277–285.

KIME, N. M., W. R. TURNER, AND M. J. RYAN. 2000. The transmission of advertisement calls in Central American frogs. Behavioural Ecology 11:71–83.

KOTLER, B. P. 1984. Effects of illumination on the rate of resource harvesting in a community of desert rodents. American Midland Naturalist 111:383–389.

LANGEMANN, U., B. GAUGER, AND G. M. KLUMP. 1998. Auditory sensitivity in the great tit: perception of signals in the presence and absence of noise. Animal Behaviour 56:763–769.

LAROM, D., M. GARSTANG, K. PAYNE, R. RASPET, AND M. LINDEQUE. 1997. The influence of surface atmospheric conditions on the range and area reached by animal vocalizations. Journal of Experimental Biology 200:421–431.

LIMA, S. L. 1988a. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53:3–11.

LIMA, S. L. 1988b. Vigilance during the initiation of daily feeding in dark-eyed juncos. Oikos 53:12–16.

LUTTON, L. M. 1975. Notes on the territorial behavior and response to predators of the pika, Ochotona princeps. Journal of Mammalogy 56:231–234.

MACARTHUR, R. A., AND L. C. H. WANG. 1973. Physiology of thermoregulation in the pika, Ochotona princeps. Canadian Journal of Zoology 51:11–16.

MacArthur, R. A., and L. C. H. Wang. 1974. Behavioral thermoregulation in the pika, *Ochotona princeps*: a field study using radio-telemetry. Canadian Journal of Zoology 52:353–358.

McKechnie, A. M., A. T. Smith, and M. M. Peacock. 1994. Kleptoparasitism in pikas (*Ochotona princeps*)—theft of hay. Journal of Mammalogy 75:488–491.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:17–34.

Naguib, M, G. M. Klump, E. Hillmann, B. Griessmann, and B. Tiege. 2000. Assessment of auditory distance in a territorial songbird—accurate feat or rule of thumb. Animal Behaviour 59:715–721.

Orr, R. T. 1977. The little-known pika. Macmillan Publishing Company, Inc., New York.

Richards, D. G., and R. H. Wiley. 1980. Reverberations and amplitude fluctuations in propagation of sound in a forest: implications for animal communication. American Naturalist 115:381–399.

Roach, W. J., N. Huntly, and R. Inouye. 2001. Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows. Oikos 92:315–324.

Roberts, G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour 57:1179–1182.

Ryan, M. J., and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126:87–100.

Schneider, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. Ecology 65:1820–1827.

Smith, A. T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55:1368–1376.

Smith, A. T., and M. L. Weston. 1990. *Ochotona princeps*. Mammalian Species 352:1–8.

Smith, J. C. 1979. Factors affecting the transmission of rodent ultrasounds in natural environments. American Zoologist 19:432–442.

Somers, P. 1973. Dialects in southern Rocky Mountain pikas, *Ochotona princeps* (Lagomorpha). Animal Behaviour 21:124–137.

Treves, A. 2000. Theory and methods in studies of vigilance and aggregation. Animal Behaviour 60:711–722.

White, K. S., W. J. Testa, and J. Berger. 2001. Behavioral and ecologic effects of differential predation pressure on moose in Alaska. Journal of Mammalogy 82:422–429.

Wiley, R. H., and D. G. Richards. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 132–181 in Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York.