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We examined the relationship between habitat structure and alarm call characteristics in six colonies of Gunnison's prairie dogs (*Cynomys gunnisoni*) near Flagstaff, Arizona, before and after a mid-summer vegetation change. We found significant differences in alarm call characteristics between colonies, confirming the existence of alarm call dialects. Differences in frequency components but not temporal components of calls were associated with differences in habitat structure. Playback experiments revealed that differences in alarm call structure affected acoustic transmission of calls through the local habitat. Thus, we identify habitat structure as one factor that may contribute to alarm call differences between colonies of Gunnison's prairie dogs. Relationships between call characteristics and habitat structure changed over seasons. Playback experiments suggested that this changing relationship could reflect a change in the purpose of the alarm call between early and late summer. Some components of alarm calls seem tailored for attenuation over short distances in the early summer but for long-distance transmission at summer's end. These differences might arise because pups stay close to their natal burrows in the early summer and disperse throughout a colony in late summer. Alternatively, these differences in alarm call transmission between seasons could be caused by the increase in vegetation in the mid-summer. At the end of the summer prairie dogs could be more dependent on long-distance antipredator calls to offset the loss of visibility caused by the increase in vegetation in the late summer. *Key words:* alarm calls, communication, *C. gunnisoni,* dialects, habitat structure, prairie dogs. *[Behav Ecol 13:844–850 (2002)]*

Dialects are variations in vocal signals between different populations of the same species. Dialects are well known among a wide variety of organisms from white-crowned sparrows (Marler and Tamura, 1962) to elephant seals (LeBouf and Peterson, 1969). Although there is evidence that dialects exist in species, there is less certainty about what factors contribute to the formation and persistence of dialects (Date and Lemon, 1993; Ryan and Brenowitz, 1985).

A combination of genetic, cultural, and environmental factors may contribute to dialect formation in most species. If sufficient genetic isolation exists between populations or if acoustic signals involve much learning from one individual to the next, genetic and cultural factors can have a strong impact on the formation of dialects (Baker, 1975; Handford and Lougheed, 1991; Somers, 1973). If different populations of the same species live in dissimilar habitats, then habitat structure can have a strong influence on dialect formation (Date and Lemon, 1993; Morton, 1986; Rothstein and Fleischer, 1987; Tubaro and Segura, 1995).

Morton (1975), Hansen (1979), and Marten and Marler (1977) first showed that habitat structure affects sound transmission, which in turn influences the evolution of acoustical signals in animals. The local adaptation hypothesis (Morton, 1975), the ranging hypothesis (Morton, 1986), and the closely related acoustical adaptation hypothesis (Hansen, 1979; Rothstein and Fleischer, 1987) were developed from these observations. The local adaptation hypothesis proposes the evolution of acoustic signals that optimize sound transmission over maximum distances (Morton, 1975). The ranging hypothesis and the acoustical adaptation hypotheses propose that some calls are selected for long-distance transmission, while other calls may be structured to predictably degrade for the purpose of establishing territory boundaries or to reduce the chance of attracting predators or competitors (Brown and Handford, 1996; Marler, 1955; Morton, 1986). All of these hypotheses stem from the common idea that local acoustic habitats are highly variable due to the interplay of atmospheric, vegetative, and ground effects. This variability causes differences in sound transmission and ultimately drives selection for unique acoustic dialects.

The acoustic environment affects vocal signals through attenuation and distortion. Animals respond to the distortion and attenuation present in the environment by changing temporal and frequency components of acoustic signals. For example, distortion of sound is related to the length of the sound. So, in less vegetated habitats, acoustic signalers often use short pulses with higher rates of repetition to avoid distortion by atmospheric effects, whereas long whistles are used in highly vegetated environments to avoid reverberation off vegetation (Handford and Lougheed, 1991).

Attenuation of sound is strongly dependent on frequency (Morton, 1975). Generally, frequencies between 1 and 4 kHz travel farthest and with most consistency in any environment (Marten and Marler, 1977). However, acoustic signalers use a much larger range of frequencies than 1–4 kHz. Ultimately, frequencies that are optimum for different habitats depend on the purpose of the signal, the balance between vegetative cover and atmospheric turbulence, and the height above the ground at which a signal is transmitted (Linskens et al., 1976; Marten and Marler, 1977; Shy, 1983; Tubaro and Segura, 1995; Waas, 1988; Wasserman, 1979; Wiley and Richards, 1978).

In this study we explored the effects of habitat structure on acoustic dialect formation in Gunnison's prairie dogs (*Cynomys gunnisoni*). Gunnison's prairie dogs are colonial, ground-dwelling rodents found throughout the grasslands of the Colorado Plateau in western North America (Hall and Kelson, 1959). Prairie dogs use alarm calls to detect and avoid predators, and the presence of nepotism in alarm calling has been documented in both black-tailed prairie dogs, *C. ludovicianus,*

and *C. gunnisoni* (Hoogland, 1995, 1996). Alarm call dialects of Gunnison's prairie dogs exist on both regional and local scales (Slobodchikoff and Coast, 1980; Slobodchikoff et al., 1998).

Although dialects are present between colonies of Gunnison's prairie dogs, it is unclear what contributes to this intraspecific variation. On a regional scale, colonies that are farther apart contain greater differences in call characteristics, suggesting that genetic isolation contributes to differences in alarm call structure (Slobodchikoff et al., 1998; Travis et al., 1997). However, on a local scale there is no relationship between distance between colonies and differences in alarm calls, suggesting that other factors are influencing local dialect formation (Slobodchikoff and Coast, 1980; Slobodchikoff et al., 1998).

Habitat structure can be extremely variable between prairie dog towns in the vicinity of Flagstaff, Arizona, USA, which may cause differences in alarm call dialects between colonies (Slobodchikoff et al., 1988). Furthermore, because of the existence of late summer monsoons, vegetation on the same colony can increase drastically from early to late summer, which may cause calls within the same colony to change between seasons. We hypothesized that habitat structure influences variations in alarm call structure in Gunnison's prairie dogs on a local scale. Specifically, we predicted that differences in vegetation cover influence both temporal and frequency characteristics of alarm calls in Gunnison's prairie dogs.

METHODS

We studied six colonies of Gunnison's prairie dogs (*C. gunnisoni*) located near the city of Flagstaff, Arizona. All colonies were located at the same elevation (2100 m) within alpine meadows surrounded by a zone of ponderosa pine (*Pinus ponderosa*). To determine whether differences in vegetative cover explained differences in alarm call dialects between colonies of Gunnison's prairie dogs, we conducted habitat analysis, recording, and playback sessions on all six colonies between May and September 1999.

Northern Arizona has a heavy monsoon season in late summer, which results in a dramatic increase in vegetation on most colonies. To establish whether prairie dogs change call characteristics in response to seasonal changes in vegetative cover, we conducted two sets of habitat analysis, recording, and playback sessions (premonsoon: 15 May–30 June 1999 and postmonsoon: 1 August–15 September 1999).

Variation in alarm calls

To determine if there were dialect differences between colonies, we recorded and analyzed alarm calls of 10–12 different prairie dogs from each colony in premonsoon season ($n = 65$) and alarm calls from 10–12 different prairie dogs from each colony in postmonsoon season ($n = 60$) for a total of 125 alarm calls from different adult prairie dogs in both seasons. Recording sessions always took place between 0630 and 0930 h to minimize variation in atmospheric conditions. Calls were recorded on high-fidelity audiotape using a Sennheiser ME-88 directional microphone (frequency response: 5–15 kHz sensitivity: 5mV/Pa) connected to a Sony TC-D5PRO II cassette recorder (frequency response: 40–15 kHz).

To minimize the possibility of recording the same prairie dog twice, we marked the burrow where the prairie dog was calling from with a plastic flag, and no further alarm calls were taken from that burrow in premonsoon or postmonsoon seasons. Although marking all prairie dogs in all six towns would have been the optimum method, we were constrained by time. We had to finish the first recording session before the rains of the monsoon season started, and the sizes of the study colonies (>100 individuals each) prohibited us from trapping and marking all prairie dogs in time. The large size of these colonies likely served to decrease the probability of sampling the same prairie dog twice.

All alarm calls were elicited by the same human adult female, dressed in the same clothes. Humans have been regularly used in alarm call studies of Gunnison's prairie dogs because approaches can be standardized more effectively than if wild or captive nonhuman predators were used (Slobodchikoff et al., 1991). Humans have hunted prairie dogs in the Flagstaff area for hundreds of years, and prairie dogs regularly alarm call in response to all humans as they would to any other predator (Slobodchikoff et al., 1991). Hopi and Navajo tribes near Flagstaff have culinary recipes for prairie dogs (Gorman, 1981), and white settlers have treated prairie dogs as pests and intensively eradicated them by hunting and poisoning for more than 150 years (McNulty, 1971). Sportsmen in the area regularly shoot prairie dogs to this day. The mean generation time for Gunnison's prairie dogs is 1.5 years, which means that at least 100 generations of prairie dogs (not including those hunted by early native Americans) have had contact with humans that kill them (Rayor, 1985). Thus, we believe that a human subject is sufficient to elicit real alarm calls from prairie dogs.

We analyzed recorded alarm calls using the RTS real-time spectogram computer package (version 3.0; Engineering Design, Belmont, Massachusetts). Frequency resolution for each spectograph was set at 48.8 Hz, and sample rate was set at 25 kHz. We analyzed six different call variables for each alarm call. Three of these six call variables were temporal variables (syllables per bout, syllable length, and interval length). A bout was defined as a series of one or more calls followed by at least 3 s of silence by the individual animal (Waring, 1970). Three frequency variables were also measured (maximum, dominant and fundamental frequencies). Maximum, dominant, and fundamental frequencies were defined as the highest, mid-range, and lowest frequencies of the call, respectively, that had higher sound intensities than the surrounding harmonic frequency bands.

We analyzed 1-s time intervals of each call sequence using RTS. Time and frequency coordinates were digitized from points on each call and were used to calculate the above six variables (Figure 1). Fundamental, dominant, and maximum frequencies all have higher amplitudes than the harmonic frequencies existing in between the main frequencies. On the RTS color display the fundamental, dominant, and maximum frequencies were easily identified by their dark red or orange color, as opposed to the lighter yellow color of the other harmonics. In cases where the difference in intensity was difficult to differentiate from the color spectograph, we converted the call to a display graph that showed amplitude versus frequency and identified the main frequencies as those with the highest amplitudes on the graph. We used ANOVA to determine if calls differed between colonies in the pre- and postmonsoon seasons as well as between the same colony in different seasons.

Relating habitat structure and alarm call differences

To quantify differences in vegetative cover, we recorded percent vegetative cover using 40 plots at each colony. Each plot was 1 m². The plots were further divided into 100 10 × 10 cm squares to aid in accurately estimating percent cover. To test for differences in vegetative cover between colonies in the same season, we used ANOVA. To determine differences in vegetation within the same colony between seasons, we performed a repeated-measures ANOVA.
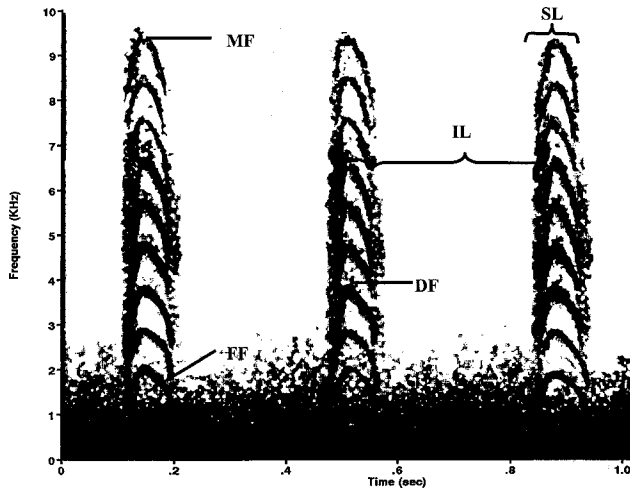
Figure 1
A spectograph of a prairie dog alarm call in response to a female human subject at Rain Valley colony. A 1-s time interval is shown. The labeled points are the call variables digitized for sound analysis. MF = maximum frequency, FF = fundamental frequency, DF = dominant frequency (frequencies identified by sound intensity, not shown), IL = interval length, SL = syllable length, SB = number of syllables per bout with a bout ending when there are 3 s of silence.

To test whether alarm call differences were related to differences in vegetative cover, we ran a regression between alarm call characteristics and percent vegetation cover (Bonferroni adjustments made: premonsoon: $\alpha/4 = 0.013$, postmonsoon: $\alpha/3 = 0.017$). We used alarm call characteristics that differed between colonies in the regression analysis. We used mean values for call characteristics and habitat cover for each colony.

To determine if differences in call characteristics affected the transmission of a call through different environments, we conducted playback experiments. Because frequency components of calls were the only call components related to differences in vegetative cover, we only tested frequency components in the playback experiments. We did this by measuring the attenuation of frequency components of calls through different amounts of vegetative cover.

The playback tape we used consisted of a 4-kHz pure tone and also a representative call from each of the six study colonies. One playback tape was made for each season and played back on all six colonies. Calls belonging to the colony where they were played back were labeled reference calls. Calls not belonging to the colony at which they were played back were labeled foreign calls. If calls played on their home territory outperformed foreign calls and if calls played on their home territory transmitted better than when they were played on foreign territories, this would provide preliminary evidence that calls may be adapted for a specific environment and purpose.

We conducted playbacks on a 100-m transect from the burrow of the representative caller for that colony. The recording tape recorder was placed at 1, 5, 20, 40, 60, 80, and 100 m along the transect line. The broadcasting tape recorder (Sony TC-D5PRO II) was attached to a Realistic MPA-25, 20-watt mobile amplifier and loudspeaker (frequency response: 275–14 kHz). This broadcasting system was placed at the caller's burrow at a height of 25 cm (the height of a calling prairie dog) and in the direction the caller had been facing (Slobodchikoff and Coast, 1980). The recording microphone was set at a height of 10 cm (the height of a listening prairie dog; Slobodchikoff and Coast, 1980). For consistency, we used the

same recording system in the sound transmission experiments that was used to record the original calls.

We standardized the sound decibel level of the playbacks between colonies by calibrating the system to 45 dB, 10 m away from the source. This calibration was used to mimic the actual sound level of an alarm call (Slobodchikoff and Coast, 1980). The 4-kHz pure tone was synthesized using an NCH tone generator (NCH Audio Action Software, 1999 version) and was used as a control to represent the average dominant frequency of prairie dog alarm calls.

We analyzed playback recordings using Signal, a computer sound analysis program (version 3.0; Engineering Design). We measured attenuation of fundamental frequencies, dominant frequencies, maximum frequencies, and the pure tone on a power spectrum (dB-volts) and converted to absolute dB SPL. Excess attenuation (EA) was then calculated for the 4-kHz pure tone and for each frequency component for all reference calls and foreign calls by subtracting attenuation due to spherical spread: 20 log(far distance/near distance) from original attenuation figures (Marten and Marler, 1977). EA in decibels at 100 m was used on dominant frequency components of the alarm call, but because other frequencies did not travel the entire 100 m, we calculated EA over shorter distances for maximum frequencies and fundamental frequencies (20 m for maximum and 60 for fundamental frequencies).

We used only one representative call from each colony for each season for the playback tape. Although randomly picking a representative call is a common practice (Hurlbert, 1984), there may be issues with pseudoreplication using this method (Kroodsma, 1989; Searcy, 1989). We dealt with this problem by using a blocked design for our ANOVA. This more conservative ANOVA is designed to handle repeated sampling methods (Sokal and Rohlf, 1995).

RESULTS

Variation in alarm calls

Alarm call dialects existed between colonies in both seasons. In the premonsoon season maximum frequency, dominant frequency, fundamental frequency, and syllable length were significantly different between colonies (ANOVA, df = 5, 69; maximum frequency: $p < .0001$, $F = 45.68$; dominant frequency: $p < .0001$, $F = 13.836$; fundamental frequency: $p < .0001$, $F = 9.06$, syllable length: $p < .0001$, $F = 7.77$: interval length and syllables per bout: $p > .056$ for both, > 2.29 for both). In the postmonsoon season maximum frequency, dominant frequency, and fundamental frequency differed between colonies, but no temporal components were significantly different (ANOVA df = 5, 64; maximum frequency: $p < .0001$, $F = 5.80$; dominant frequency: $p < .0001$, $F = 5.22$; fundamental frequency: $p < .0001$, $F = 6.57$; syllable length, interval length, syllables per bout: $p > .09$ for all, $F < 2.02$ for all).

There were significant differences in maximum and dominant frequencies within the same colony, between seasons (ANOVA, season effect: $p < .0001$, $F = 52.67$, df = 1,6: maximum frequency: $F = 93.97$, $p < .0001$, df = 1,6; dominant frequency: $F = 18.33$, $p < .0001$, df = 1,6). However, no other call components changed within the same colony between seasons (ANOVA, season effect: fundamental frequency: $F = .892$, $p = .347$, df = 1,6; syllable length, interval length, syllables per bout: $F < .92$, $p > .34$, df = 1,6 for all).

Relating habitat structure and alarm call differences

Habitat structure was different both within and between our study colonies. There were significant differences in vegetative

a.)

b.)

c.)

d.)
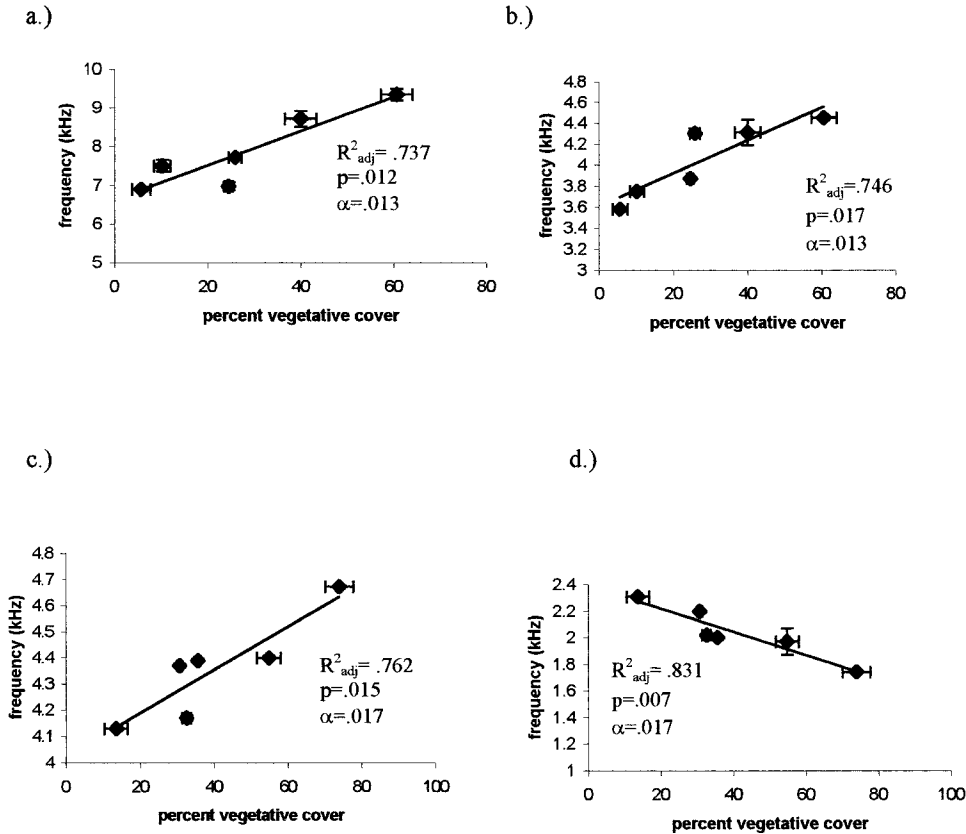
Figure 2
Regressions of mean percent cover against selected frequency components for each colony. (a) Maximum frequency in premonsoon, (b) dominant frequency in premonsoon, (c) dominant frequency in postmonsoon, and (d) fundamental frequency in postmonsoon. Adjusted R^2 values and Bonferroni-adjusted alpha levels are shown. Error bars represent 1 SE.

cover between colonies throughout the study period (ANOVA, premonsoon: $p < .0001$, $F = 80.31$, df $= 5,239$; postmonsoon: $p < .0001$, $F = 67.5$, df $= 5,239$). In addition, percent cover changed significantly within the same colony between premonsoon season and postmonsoon season (repeated-measures ANOVA by season: $p < .0001$, $F = 103.05$, df $= 5,234$).

If the observed differences in habitat structure on our study colonies affect dialect differences between colonies, we would expect that colonies with more similar vegetation structures would have more similar alarm calls. In the premonsoon season, dominant frequencies, fundamental frequencies, maximum frequencies, and syllable lengths differed between colonies. However, only maximum frequency was influenced by differences in habitat structure (regression, Bonferroni corrected $\alpha = .013$: $R^2_{adj} = .737$, $p = .012$, $F = 19.07$, df $= 5$; Figure 2a). Dominant frequency, fundamental frequency, and syllable length were not significantly related to habitat differences (regression, Bonferroni corrected $\alpha = .013$, df $= 5$ for all: dominant frequency: $R^2_{adj} = .746$, $p = .017$, $F = 15.71$, Figure 2b; fundamental frequency: $R^2_{adj} = .006$, $p = .367$, $F = 1.03$; syllable length: $R^2_{adj} = -.230$, $p = .811$, $F = .065$). Thus, observed differences in vegetation cover explain some but not all of the dialect differences that we observed in the premonsoon season.

It is interesting that the relationship between vegetation cover and alarm call characteristics changes with season. In the postmonsoon season, dominant frequency and fundamental frequency of alarm calls were significantly associated with vegetative cover (regression, Bonferroni corrected $\alpha = .017$: dominant frequency: $R^2_{adj} = .762$, $p = .015$, $F = 17.00$, df $= 5$; fundamental frequency: $R^2_{adj} = .831$, $p = .007$, $F = 25.58$, df $= 5$; Figure 2c,d). However, variation in maximum frequency was not explained by habitat in postmonsoon season (regression, Bonferroni corrected $\alpha = .017$: $R^2_{adj} = .569$, $p = .051$, $F = 7.61$, df $= 5$).

Playback experiments revealed that statistically significant relationships between call characteristics and habitat cover translated into real differences in transmission performance of calls through the environment. In the premonsoon season, there was no difference in the excess attenuation of reference calls and foreign calls for fundamental and dominant frequencies, but the EA of maximum frequency was significantly greater in reference calls compared to foreign calls (ANOVA randomized complete block design, Bonferroni corrected $\alpha = .017$: maximum frequency: $F = 6.27$, $p = .016$, df $= 5,24$; fundamental frequency, dominant frequency, $p > .05$; Figure 3a). Unexpectedly, this means that maximum frequencies did not travel as far on home colonies as they did on foreign colonies in the premonsoon season.

Similar to premonsoon season, those call characteristics that were related to habitat variation in postmonsoon season also showed significant differences in actual transmission performance through the environment. However, postmonsoon frequencies of reference calls attenuated less (traveled farther) than foreign calls. Both fundamental and dominant frequencies in reference calls experienced significantly less EA than foreign calls (ANOVA randomized complete block design, Bonferroni corrected $\alpha = .017$: dominant frequency: $F = 7.14$, $p = .008$, df $= 5,24$; fundamental frequency: $F = 7.59$, $p = .011$, df $= 5,24$; maximum frequency: $F = .097$, $p = .758$, df $= 5,24$; Figure 3b).

In summary, there were differences in alarm calls both between colonies and within the same colony over seasons. Both seasons revealed relationships between habitat and frequency aspects of calls; however, the relationship changed with season. Finally, the statistically significant relationship between habitat structure and call frequencies was supported by differences in actual transmission performance of those frequencies through different environments.
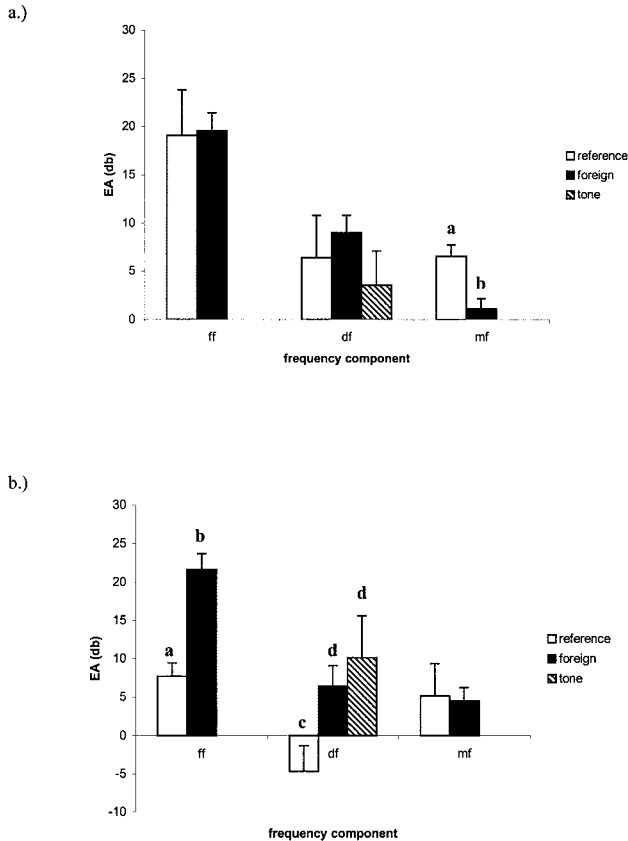
a.)

b.)

Figure 3
Excess attenuation (EA) is compared among reference calls, foreign calls, and a pure tone. (a) Premonsoon: a,b = significant difference between (maximum frequency) of reference calls and foreign calls; ANOVA complete randomized block design, α = .017, p = .016. There are no other significant differences. (b) Postmonsoon: Letters = significant difference between call categories (ANOVA complete randomized block design, α = 0.017; dominant frequency of reference vs. foreign, p = .008, dominant frequency of reference vs. pure tone, p = .013, fundamental frequency of reference vs. foreign, p = .011). Error bars represent 1 SE.

DISCUSSION

The variation we uncovered in alarm calls between colonies supports the hypothesis that alarm call dialects exist in Gunnison's prairie dogs (Slobodchikoff and Coast, 1980; Slobodchikoff et al., 1998). To be classified as dialect differences, alarm calls within a colony would need to be consistently more similar to each other than to alarm calls from different colonies. The alarm calls of Gunnison's prairie dogs did change within a colony through seasons. However, despite these internal changes, alarm calls within the same colony were consistently more similar to each other than they were to alarm calls of prairie dogs in other colonies.

Our study suggests that dialects in Gunnison's prairie dogs are at least partially influenced by differences in vegetative cover. This is consistent with other studies that have found relationships between habitat cover and structure of acoustic signals (Date and Lemon, 1993; Handford and Lougheed, 1991; Slobodchikoff and Coast, 1980; Waas, 1988; Wasserman, 1979). However, although habitat structure does appear to influence dialects, it is clearly not the only factor constraining dialect formation and persistence.

Differences in temporal aspects of alarm calls were not associated with habitat differences. Other forces that regularly

drive dialect selection, such as genetic isolation (Baker, 1975) or cultural influences (Handford and Lougheed, 1991), could influence temporal components of alarm calls. For example, both frequency and temporal components of dialects in pikas are highly influenced by genetic isolation (Somers, 1973). In addition, other measures of habitat structure that we did not evaluate in this study could affect call components. For example, stem diameter of vegetation, wind patterns, and humidity may heavily influence components of acoustic signals in open grassland environments (Richards and Wiley, 1980; Wiley and Richards, 1978).

Frequency components of calls were clearly influenced by habitat structure, and attenuation differed depending on frequency levels used. This leads us to question how vegetative cover affects transmission of different frequencies. Attenuation of sound is highly dependent on frequency (Morton, 1975). Wiley and Richards (1978) suggested that wavelengths of vocal signals may be fine-tuned to the diameter of plants and air pockets in the local environment, allowing for least attenuation (see also Richards and Wiley, 1980). Wavelength is proportional to frequency, with shorter wavelengths producing higher frequency sounds. As vegetation cover changes, the diameter of plants and air pockets may change, leading to more optimal use of slightly different frequencies. The mechanics of sound propagation through vegetation are extremely complex, but future studies that are designed to isolate the cause of the relationships between frequency and habitat structure would provide an appealing next step to this study.

Perhaps the most interesting and puzzling result of this study is the seasonal change in the relationship between habitat structure and call characteristics. The relationship between habitat and maximum frequencies of calls in the premonsoon season actually produced calls that attenuated more strongly on home colonies than on foreign colonies. In postmonsoon season, we observed the opposite. Dominant and fundamental frequencies attenuated less on home colonies than on foreign colonies. Why did we find this changing relationship between habitat structure and alarm call structure? The adaptation of an acoustic signal to its local acoustic environment depends on the purpose of the signal as well as on the physical structure of the acoustic environment. In some cases, acoustic signals will be selected for optimizing sound transmission over maximum distances (Morton, 1975). However, some signals may be structured to predictably degrade for the purposes of establishing territory boundaries or reducing the chance of attracting predators or competitors (Brown and Handford, 1996; Marler, 1955; Morton, 1986).

When looked at from this perspective, the different attenuation performances of frequencies suggest that alarm calls could be designed for different purposes that change seasonally. Specifically, certain call components may be designed for maximum travel in postmonsoon season and degradation over short distances in premonsoon season. Gunnison's prairie dog alarm calls contain specific information on predators (i.e., type, danger level, hunting style), and frequency components of calls carry this information (Placer and Slobodchikoff, 2000, 2001; Slobodchikoff et al., 1991). Little is known about the actual coding of the information in the calls. However, differential attenuation of certain frequencies in a call could provide extra information about predators.

We cannot conclusively relate seasonal changes in the call–habitat structure relationship to changes in call purpose without conducting studies that relate changes in alarm calls to fitness levels. However, we do offer some hypotheses. Premonsoon season corresponds to the time when pups emerge from their natal burrows. Prairie dogs live in spatially and temporally fixed territories within the colony, and pups reside in

their natal territory until dispersal at the end of the summer (Robinson, 1989; Travis and Slobodchikoff, 1993). Perhaps quickly degrading alarm calls in the premonsoon season are directed toward the more vulnerable pups. Hoogland (1996) suggests that alarm calling in Gunnison's prairie dog females is primarily an expression of parental care. The cost of calling long distances in the premonsoon seasons could be too high, as it draws the attention of predators to the area of the caller where the pups reside. Alarm calls that degraded quickly could lower the cost of calling. Calling with lower amplitude might have the same effect of lowering the cost of detection by predators. However, alarm calls in which the maximum frequency drops out quickly would have a narrower bandwidth, which would cause them to be less locatable even at a short distance. Alarm calls of birds contain narrow bandwidths of frequencies that increase inconspicuousness and decrease predator detection (Marler, 1955).

Thus, in the premonsoon season, calls with maximum frequencies that carried shorter distances would have narrower bandwidths at a distance, yet contain the full amount of information at close range. This may serve to warn pups while minimizing the chance that a predator could hear and locate the call. In the postmonsoon season juveniles disperse away from their natal territory (Robinson, 1989). This could alleviate the need for calls that degrade over short distances and promote calls that carry long distances in postmonsoon season.

In addition to the decreased cost and increased benefit of calling over long distances in postmonsoon season, alarm calls that carry long distances could be tied to the decrease in visibility experienced with the increase in vegetation after the monsoon. As a whole, vegetation cover increased between pre- and postmonsoon season and was taller than the height of most prairie dogs. Perhaps decreased visibility makes prairie dogs more dependent on acoustical communication for predator detection and avoidance in this season. Higher selection pressure on acoustic signals in habitats that are less visibly open has been shown in populations of Old World monkeys. Brown and co-workers (1995) found a higher incidence of acoustic signals modified for long-distance travel in species residing in low-visibility areas such as forests. In contrast, savanna monkeys, residing in high-visibility areas, did not have acoustic signals fine-tuned for long-range communication.

Ultimately, in order to say that habitat structure influences the design of alarm calls, the functionality of the alarm call structure in terms of fitness needs to be described. The fact that alarm call frequencies differ in relation to habitat (both between colonies and seasonally within the same colony) and that this results in actual differences in attenuation through different environments is a first step in discovering functionality of alarm calls. As a first step, we can point to the fact that there is a relationship between frequency components of alarm call dialects and vegetative cover. We can also say that this relationship affects the transmission of the alarm call through the environment, which implies that calls may be adapted to home environments. Most studies examining the influence of habitat on acoustical signals investigate territory advertisement, species recognition, and mating songs (e.g., Baker, 1975; Morton, 1986; Wiley, 1991). Further research on the relationship between habitat structure and prairie dog alarm calls has the potential to incorporate new and different selection pressures such as kin selection and predation into the study of the effects of habitat on acoustical communication.

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