Kalahari Soundscapes: The Functional Significance of Large Carnivore Vocalizations

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Introduction

The 2014 Sound in the Land festival/conference sought to explore and discover new ways of hearing the earth, listening to the environment, and creating musical and scholarly responses to what we hear. This, in essence, is "ecomusicology"—the study of music, culture, and environment in all their complexities. It considers musical and sonic issues, both textual and performative, related to ecology and the natural environment.[1] This concept dovetails with another important concept, that of biodiversity. Biodiversity should not be interpreted simply as implying species richness or species diversity. It is a broad concept incorporating compositional, structural, and functional attributes at different levels in the ecosystem, namely landscapes, communities, species, and genes.[2]

My research in the Kalahari aims at understanding functional relationships between the environment and predators and their prey, and also relationships among the predators themselves. In this paper I discuss some of these relationships within an ecomusicology framework, using four species of large carnivores as examples: two cats and two hyenas, one each of which is more solitary and the other highly social. The cheetah *Acinonyx jubatus* is the solitary cat; the lion *Panthera leo* is the social cat. The brown hyena *Hyeana brunnea* is the more solitary hyena; the spotted hyena *Crocuta crocuta* is the social one.

The Kalahari

The Kgalagadi Transfrontier Park, located in the Kalahari regions of both Botswana and South Africa, is a pristine area of 38,000 square kilometers

1 *The Grove Dictionary of American Music* (Oxford: Oxford Univ. Press, 2014).

2 R.F. Noss, "Indicators for Monitoring Biodiversity—a Hierarchical Approach," *Conservation Biology* 4 (1990): 353-54.

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(14,670 square miles) in the southern, most arid, part of the Kalahari. The Kalahari is a large, sand-filled basin, with the sand in this region piled into linear or seif dunes fixed by vegetation. Annual rainfall in the study area is approximately 220 mm (nine inches). Two riverbeds run through the area, but they only flow for short periods and distances during abnormally wet years. There is no naturally occurring permanent water in this area, and all animal inhabitants, including the large carnivores, are adapted to survive without surface water. The vegetation is predominantly shrubby grassland, except along the riverbeds where an open tree savannah is found. Ecological conditions dictate that herbivorous animals are generally thinly distributed and need to be mobile. One of the major biodiversity characteristics of the Park is that it is a relic of a large herbivore nomadic community in an arid ecosystem, supporting a functional large carnivore predator/prey system.

Cheetah

The cheetah is a solitary cat. Females raise their cubs alone; however, about half the adult males form strong and long-lasting coalitions like those established among male lions (no other cats do this), usually of two or three members. Female cheetahs are not territorial, and infanticide is not an issue for female cheetahs to contend with.[3] The call of the female to her cubs and vice versa is a soft, uncat-like sound, more like the chirp of a bird. It does, however, carry over a surprisingly long distance. It is well-suited to the function of conveying to each other their whereabouts after a separation, without drawing the attention of potential predators such as lions and spotted hyenas. Mother and cubs, and coalition males, also purr loudly when socializing and cleaning each other's faces after feeding.

When searching for a female in heat, male cheetahs may advertise their presence with a louder stutter-like, churtling call. There is risk involved in this, as the call may attract other males in the vicinity who are also searching for the female. This is likely to result in aggressive behavior. On one occasion our research team witnessed a two-male coalition attack and kill a single male which had inadvertently attracted other males in this way.

[3] David W. Macdonald, Andrew J. Loveridge, and Kristin Nowell, "Dramatis Personae: An Introduction to the Wild Felids," in *Biology and Conservation of Wild Felids,* ed. David W. Macdonald and Andrew J. Loveridge (Oxford: Oxford Univ. Press, 2010), 3-58.

Lion

Of thirty-six species of wild cat in the world, the lion is the only one that is truly social. Adult females form stable groups known as prides. These groups consist of several related females and their offspring which are raised communally. They are joined by less permanent adult male members; occasionally a single one, but in the Kalahari usually coalitions of two to three, and even more in other, more fertile areas. Members of a coalition share the same status and protect females and their cubs from other infanticidal males which may invade the pride territory. Should a new coalition manage to evict the males from a pride, they will kill the cubs. The females then come into heat and mate with the new males. In this way the males ensure that the cubs they are protecting are their own, and the females have the protection of the strongest males to ensure that their cubs survive.[4]

Lions, like other big cats of the genus *Panthera*—the tiger *Panthera tigris*, jaguar *Panthera onca,* and leopard *Panthera pardus*—can roar loudly and deeply because of adaptations to their vocal cords. These are flat and square in shape, loose and gel-like, and can withstand strong stretching and shearing, as air from the lungs passes through them. The tonal frequency when roaring is a function of the mechanical properties of their vocal cords, not their size.[5]

Lions are able to identify the roars of different individuals. Males roar to proclaim their presence in an area, often in unison. Intruders' roars in a territory elicit the cooperative behavior of male coalition residents. They will respond by seeking out the intruders to defend the territory.[6] Females can distinguish between the roars of resident father males, which they ignore, and unknown potentially infanticidal males, which cause them to retreat rapidly with their cubs.[7] Females also roar to proclaim territory which they

[4] Ibid.

[5] Sarah A. Klemuk, Tobias Riede, Edward J. Walsh, and Ingo R. Titze, "Adapted to Roar: Functional Morphology of Lion and Tiger Vocal Folds," PLoS ONE 6(2011): e27029. *(PLoS ONE is an international, peer-reviewed online publication that presents primary research from all scientific disciplines. – Editor)*

[6] Jon Grinnel, Craig Packer, and Anne E, Pusey, "Cooperation in Male Lions: Kinship, Reciprocity or Mutualism?" *Animal Behaviour* 49 (1995): 95-105.

[7] Karen McComb, Anne Pusey, Craig Packer, and Jon Grinnel, "Female Lions can Identify Potentially Infanticidal Males from Their Roars," *Proceedings of the Royal Society, London B*

defend against females from neighboring prides. Unlike the males, which are basically defending the females and their cubs, the females defend the food resources in the territory. They are able to assess the numerical strength of an intruding female group and, presumably, the extent of the threat. They modify their behavior depending on the numbers in the trespassing group. They respond more quickly to the roar of a single female than to the roars of several females. They tend to be more cautious and may also call in other lions from the pride when confronted by groups of unfamiliar females.[8]

Brown Hyena

The brown hyena is well adapted to arid regions.[9] It is predominantly a scavenger, supplementing its diet on wild fruits. It is blatantly solitary in its quest for food, always moving on its own, but secretly social in that it is a cooperative breeder. Several, mainly closely related, individuals share a common territory of about 300 square kilometers (116 square miles) and help to feed the cubs by carrying food to the den.[10]

The vocal repertoire of the brown hyena is limited to a series of predominantly short-distance communications, for example a whine by cubs begging for food from adults, and a hoot-laugh, signifying dominance in occasional dyadic interactions—usually between clan members—at food. The loudest sounds made are a combined yell and growl. This is heard during rare, one-on-one, ritualized territorial disputes involving neck-biting, and is made by the submissive animal.[11] To make up for this small vocal repertoire, the brown hyena has evolved an elaborate scent-marking strategy known as pasting—the secretion of complex chemical compounds onto grass stalks through anal glands. When moving through the territory, a brown hyena pastes an average of 2.65 times per kilometer (4.2 times per mile), resulting in an elaborate network of chemical messages left to others of its species.[12]

252 (1993): 59-64.

[8] Karen McComb, Craig Packer, and Anne Pusey, "Roaring and Numerical Assessment in Contests between Groups of Female Lions," *Animal Behaviour* 47 (1994): 379-87.

[9] Michael G.L. Mills, *Kalahari Hyaenas* (London: Unwin Hyman, 1990), 2.

[10] Ibid., 231-34.

[11] Ibid., 167-70.

[12] Ibid., 191.

Spotted Hyena

Although the spotted hyena, like the brown hyena, is well adapted to scavenging, it is also an efficient predator. In the Kalahari, 73 percent of the spotted hyena's food comes from its own kills.[13] Most food items provide a meal for several hyenas at one time, and for this reason spotted hyenas often forage in groups. Spotted hyenas live in larger clans than do brown hyenas. In the Kalahari, because of the scarcity of resources, clan size is comparatively small (usually 5-12) and clan territory size is large, with a mean of 1,095 square kilometers (462 square miles).[14] In more productive areas, such as the Ngorongoro Crater in Tanzania, as many as 80 spotted hyenas may live in a territory as small as 40 square kilometers (17 square miles).[15]

The spotted hyena has probably the most complex social system of any mammalian carnivore. A clan revolves around its adult females. They are socially dominant to the males and take the lead in most clan activities. Clans are arranged in a linear hierarchy in which the status of the lowest ranking female is above that of the highest ranking male. Co-operation in raising cubs does not occur; females suckle only their own cubs, and clan members do not carry food to another female's den. For the first year of its life, a cub's main source of food is its mother's milk. For this reason, female dominance is important; it assures them priority of access at carcasses, and enables them to feed quickly, convert the meat into milk, and return to the den to feed their cubs.[16]

Spotted hyenas live in fission/fusion societies, where members change group composition and size often and rapidly, depending on circumstances. They may be found alone when out scavenging, in a hunting group of several, or in a group of a dozen or more to defend the territory against an incursion from a neighboring clan or an interspecific clash with lions, their major competitors.[17]

In order to accommodate this complex social system, the spotted

[13] Ibid., 35.
[14] Ibid., 165.
[15] Hans Kruuk, *The Spotted Hyena* (Chicago: Univ. of Chicago Press, 1972).
[16] Marion L. East and Heribert Hofer, "*Crocuta crocuta* Spotted Hyaena," in *Mammals of Africa* Vol. 5, ed. Jonathan Kingdon and Michael Hoffmann (London: Bloomsbury, 2013), 273-81.
[17] Ibid.

hyena has evolved a number of communal and long distance vocalizations.[18] One of the best known is the whoop. Two structurally distinct types of whoop are made: 1) asymmetrical, which produce a lowing sound that ends abruptly with an increase in pitch, and 2) symmetrical, which also start with a lowing sound that rises in pitch but then returns to the initial lowing sound. Each whooping bout contains about nine individual whoops. There is considerable variation between individuals in the structure and number of harmonics in the whoop, and experiments have shown that hyenas, like lions, can recognize callers individually, since the structure and harmonics of the whoop of the same individual remain constant over several years.[19]

Two main functions of whoops are recognized. The first is a display of identity. This is particularly important for males. Because of the polygamous mating system and dominance hierarchy among males, whooping serves to advertise status. Dominant males exert more effort than low-ranking males when whooping. They have higher display rates, more often use the energetically costly symmetrical whoop, and produce more calls per bout. This may serve as an honest signal to the females of a male's evolutionary fitness.[20] In effect, the males are saying to the females: "Look how much energy I can spend on advertising myself. I have good genes and so you should choose me as a mate."

The second major function of the whoop is as a rallying call, and is more often used by females. Females whoop collectively in agonistic territorial encounters between clans or when interacting with lions. This whoop is repeated more rapidly than an advertising whoop. It is a call to arms, as hyenas quickly arrive on the scene from different directions.[21] As groups form, and if the interaction escalates, a number of other vocalizations are emitted, giving rise to some of the most remarkable sounds in nature—a cacophony of whoops, yells, howls, lows, and growls. These group displays

[18] Mills, *Kalahari Hyaenas*, 180.

[19] Marion L. East and Heribert Hofer, "Loud Calling in a Female-dominated Mammalian Society: I. Structure and Composition of Whooping Bouts of Spotted Hyaenas, *Crocuta crocuta*," *Animal Behaviour* 42 (1991): 627-49.

[20] Marion L. East and Heribert Hofer, "Loud Calling in a Female-dominated Mammalian Society: II. Behavioural Contexts and Functions of Whooping of Spotted Hyaenas, *Crocuta crocuta*," *Animal Behaviour* 42 (1991): 651-69.

[21] Ibid.

are geared to be intimidating. The more individuals that partake, the louder and more varied are the sounds. This conveys the combined fighting power of the group to the opponents, and may serve to limit the intensity of the conflict. The smaller and/or less vocal, and therefore less confident, group might back down, thereby limiting outright aggression and the possibility that participants might become severely injured.

Conclusion

In this short account I have tried to place the sonic attributes of some remarkable animals into an evolutionary scientific framework as another way of listening to the earth. Whatever our approach and philosophical angle to life might be, I believe it is important to try to understand the underlying biological significance and function of animal behavior. Not only is such understanding empowering, it also enhances respect, and thereby our desire to conserve other forms of life besides our own.

Gus Mills, a biologist, has spent more than forty years studying large carnivores in South Africa's Kgalagadi (Kalahari) Transfrontier and Kruger National Parks.

Male Cheetah calling. Kgalagadi Transfrontier Park, South Africa, February 14, 2010.
Photo credit: Gus Mills

Lion roaring. Kgalagadi Transfrontier Park, South Africa, July 13, 2011.
Photo credit: Gus Mills

Brown Hyena cubs at their den. Kgalagadi Transfrontier Park, South Africa, July 3, 2010. Photo credit: Gus Mills

Spotted Hyena showing a hierarchy in which females dominate. Here a female chases a male while a second female keeps the food. Kgalagadi Transfrontier Park, South Africa, March 13, 2011. Photo credit: Gus Mills