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Evolution

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Project Summary Draft

Summary: Evolution of cranial appendages in the Cervidae and Bovidae families

Reconstructing phylogeny of species and their traits proves difficult without a full fossil record. Questioning the possible origins of similar traits shared by different species is integral to the process of mapping the most plausible phylogenic theories. During this process, the relation of similar traits between species be uncovered: are certain traits, that may be similar in function, anatomy or outward appearance, from the mutation of a common ancestor? Or could these traits have developed on their own?

This project explored the evolutionary development, fixation, phylogeny and compositional differences in the cranial appendages or “headgear” sported by members of the mammalian order Artiodactyla, focusing on the families Cervidae and Bovidae. Cervidae (white tailed deer, reindeer, moose, etc.) have “antlers” with multiple points that shed and regrow seasonally and are comprised of bone and velveteen skin during regrowth. Bovidae (buffalo, gazelle, sheep, etc.) have visibly different headgear: they possess “horns” that have a single point, do not regenerate if lost and are primarily made of keratin.[4] The development of these cranial appendages are still a topic of debate. Did these families attain their headgear separately through homoplasy between the two, or is the development of this feature homologous through a common ancestor? While the common ancestor between the two families is not known, looking at the key differences and similarities in headgear may provide insight. The reoccurring characteristics throughout the project focused on anatomical structure and growth as well as function in sexual selection, social dynamic, and defense.

Cervidae and Bovidae diverged around 25.5 – 27.8 million years ago. There are currently no fossils found of their common ancestor, thus, scientists cannot determine if the ancestor sported any type of headgear. In other words, homology or homoplasy cannot be concluded. The earliest recorded Cervidae with headgear is Dicrocerus (Miocene) that had a small, weak set of antlers. Despite the development in horns among Bovids, there are still fossil remains of Bovids without horns (along with extant hornless species); therefore, it is still possible that Cervidae first diverged from hornless Bovidae and later developed a different mutation that evolved into antler structures. Although the appearance of headgear, based on fossil remains, seemed to occur around the same time for families in the Artiodactyla order, that does not definitively conclude homologous evolution of horns and antlers. The mutation could have still been expressed at different times and the mutations that created horns and antlers could be entirely different, meaning a homoplastic evolution route between them.

There are the major differences in what is physically observed and the anatomical structure that gives horns and antlers reason behind their separate classifications. Bovidae horns are covered by an additional layer, or “sheath,” that is made of keratin, while antlers are entirely made of exposed bone, once a velvet layer containing blood vessels and nerves, sheds away. This velvet layer is living tissue that bleeds when injured. In contrast, horns contain no living tissue.[1][4] This difference in underlaying and inherited structure is enough to question theories of homology between horn and antler evolution. It is not so much the phenotypic expression in adulthood that sheds light on the origin of traits. Still, the difference in observed shape could be accounted for by homologous divergent evolution where the common ancestor shared a form of headgear that evolved into different structures.[6]

The differences in growth are also a significant part of inherited structural patterns. Horns are permanently attached to the skull and, if one is damaged and falls off, will never grow back. In contrast, Cervidae antlers are in a constant cycle of growing, shedding and regrowth that correlates with mating seasons. In Cervids, only males grow antlers (except reindeer where both sexes develop them) while it is more common among Bovid species for both males and females to develop horns. The development in only Cervid males points to an expression of a secondary sex characteristic, prompted by seasonal testosterone production. Females injected with testosterone began antler growth, but never developed them fully.[4] There is also evidence to suggest a correlation between the size of antlers and the male's overall health: the larger the antlers, the more weight to bear, suggesting a healthier male.[8] I hypothesized females that carry offspring cannot expend as much energy into antler-bearing, especially if antlers do not have much use in fighting. Females showed the potential for developing antlers showing they at least retained some of the antler-building structures males have, similar to the potential for horns in some female Bovids. Natural selection may have gotten rid of antlers in female Cervids but kept them in female reindeer. The potential to develop headgear in female Cervids points to homology between Cervids and Bovids, however, it would not be unreasonable to rule out homoplastic evolution; both mutations that caused antlers and horns could still be entirely different and from different ancestors.

When looking at sexual selection and behavior there are more similarities. Males will fight each other for a mate and use their headgear as weapons (the larger the better for fighting); there is status and power within group dynamics that comes with winning a fight. It is suggested, however, that both horns and antlers have become status symbols to avoid actual conflict. In sheep, the size of horns is observed to be the determining factor in hierarchy to minimalize fights for higher survival rates. This suggests that horn function is now dually used for display.[3] Horns can still be used as weapons to wield off predators if needed, which might explain the presence in both males and females for some Bovid species. Antlers are emphasized as display features because they are weak, not ideal for fighting predators, and they grow back more complex (yet not stronger for fighting predators) each year.[4][7] It appears that their interpreted functionality is analogous in some ways, but that does not necessarily point to inheritance.

Studies have shown the environment to influence the shape of antlers within the same family. Cervinae in temperate regions mate seasonally and develop more complex antlers, in comparison to those in the tropics that mate and participate in mating rituals more often.[6] If environmental influence on headgear were to be applied to Bovids as well, environment could also be a factor in a divergent evolutionary path between antlers and horns. The environment and the presence of certain predators can determine the need for either fight or flight, and even what bodily function the most energy needs to be placed in (growing headgear or rearing offspring).

The differences in external and internal structure between horns and antlers were further explored sculpted in detail and hung as a mobile: one horn and one antler made up the main body of the sculpture to show the separated Cervid and Bovid families. The branching nature of the sculpture symbolizes the structure of a phylogenic tree where moving toward the tips represents more recent history. On each, a portion was sculpted to depict the interior structures and highlight the differences: the exposed area of the antlers showed fully exposed bone and a spongey bone interior where blood vessels were located during growth while the horn side showed the solid bone core and keratin outer sheath. This difference is shown at the top of the sculpture to depict the standard structure for each type of headgear represented on either side. The main antler and horn parts were connected at the top by a thin wire, but were not sculpted together as one, to show the uncertainty behind their homology or homoplasy. Loose strings that connect the headgear at the tip further represented this uncertainty and unknown common ancestor between Cervids and Bovids. The overall branching pattern of the mobile represented the structure of a branching evolutionary tree where more recent and extant species were at the bottom tip. Each species depicted had small tags that had an image of their environment and a few key words or phrases about their habitat. These tags were important to the sculpture because they explained the possible environmental influences on the diverse headgear characteristics for each species (i.e. why selection may have favored certain shapes, sizes, growth patterns, etc.). Any species that is known or hypothesized to show aggression toward predators had a red antler/horn tip that symbolized blood.

The first level down from the top had the oldest species of Cervidae (*Dicrocerus*) and Bovidae (*Eotragus*) found to have headgear and they were hung from their respective headgear sides. Both species had a forest tag (although the exact habitat and threats they faced is not entirely known); they were small with a similar, simple set of headgear influenced by the likeliness of needing to hide from large predators or fight small ones. The next level down showed a transitional species for each family on their respective sides: *Libralces gallicus* for Cervidae and *Megalotragus* for Bovidae. The *Libralces* held a savanna tag where its large body and antler size was likely used for visibility for mating in open areas, and the large set of simple antlers may have been used for attacking predators. The *Megalotragus* had a grasslands tag and was also large compared to its extant gazelle relatives, likely using aggression against predators.

The extant species were positioned at the tips, as they are on a phylogenic tree. They hang off the main structure of the sculpture to symbolize present-day species. The first pairs represented the differences between males and females developing headgear; one of the pair is with headgear (male) and the other without (female). The headgear intertwined with another of its kind was to represent fighting for sexual selection. For Cervids: the white-tailed deer had a temperate forest tag; a smaller set of antlers for hiding from predators while females put energy into rearing young instead of antler growth. For Bovids: black Welsh mountain sheep had a herd tag; it is possible this sheep breed favors females rearing young and are more protected from predators in a herd, allowing only males to grow horns for aggression. The next level shows closely related species where both sexes grow headgear. This level is still connected to the previous one to show the genetic potential of headgear in both sexes. Both female and male reindeer grow antlers (the only Cervidae where this occurs) and that potential is expressed in female white-tailed deer that may grow antlers with the addition of certain hormones. They had a snowy terrain tag where high physical strength and energy are important in cold environments and antlers may be needed in both sexes to clear snow. The dama gazelle had a savanna tag where horns are for defense against smaller predators but are smaller in size to allow them to run in open areas from big ones.

On a larger scale, by questioning homology and homoplasy, this project explored the importance of genetic variation and mutations in ancestry that allow adaptation to environments and threats. In the case of homology; did the headgear greatly diverge to suit each family's environmental need? Or in the case of homoplasy; is the mutation for headgear a structure gravitated toward by each family, but developed separately? Through discovering the origins of traits by mapping phylogenies and pondering evolutionary possibilities, humans can, besides cater to curiosity, get insight into the way evolution works and how we interact with, relate to, and impact the environment and thus, the organisms that live within it. In the age of the so-called Anthropocene, realizing the size of human impact on generations of organisms and their ability to adapt to the changing environment is increasingly important. This project attempts to look at non-human species and pay homage to the origins of their genetic adaptations.

Bibliography

1. Evolution of ruminant headgear: a review.

- Davis, Edward Byrd, et al. "Evolution of Ruminant Headgear: A Review." *Proceedings. Biological Sciences*, vol. 278, no. 1720, Oct. 2011, pp. 2857–2865. *EBSCOhost*, doi:10.1098/rspb.2011.0938.
- This article outlines the differences between different types of cranial appendages and families that have them, such as antlers in cervids, horns in bovids, giraffids and antilocaprids. Horns are made of bone with a keratin "sheath" and never regrow if they fall off, while antlers are made entirely of bone once the velvet layer of blood vessels sheds and are a constant cycle of loss and regrowth. Similarities between horns and antlers include their symmetry and placement on the head.

2. Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences.

- Miyamoto, M M et al. "Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences" *Proceedings of the National Academy of Sciences of the United States of America* vol. 87,16 (1990): 6127-31.
- This is study comparing mitochondrial DNA sequences attained from extant subfamilies of antlered deer (Cervinae, Muntiacinae, Odocoileinae) and antlerless sister group Hydropotinae. Some of the mutations that define the variations between each species were identified. The most parsimonious solutions found support the hypothesis that antlered deer are from the same antlered ancestor (homologous). The most parsimonious solution also indicates rates of nucleotide change among antlered deer are similar and suggests odocoileines diverged from other antlered deer in Late Miocene.

3. The Evolution of Horn-Like Organs

- Geist, Valerius. "The Evolution of Horn-Like Organs." *Behaviour*, vol. 27, no. 3/4, 1966, pp. 175–214. *JSTOR*, www.jstor.org/stable/4533157.
- This article emphasizes the difference between visually observed structures within a family, such as antelopes with a wide variety of horns despite living in similar or the same environments. It also suggests that horns were (and still can be) used for fighting due to their sturdy structure, but have become more like display signs to avoid conflict and actual fighting (backing down before violence begins).

4. HORNS AND ANTLERS

- Modell, Walter. "HORNS AND ANTLERS." *Scientific American*, vol. 220, no. 4, 1969, pp. 114–123. *JSTOR*, www.jstor.org/stable/24926338.
- The article speaks on the inefficiency of antlers in fighting and defense. It further outlines the differences between horns and antlers and provides that Bovidae males and females can typically grow horns, while in most of the Cervidae only males attain them as secondary sex characteristics promoted by the hormone testosterone. The article explains a little about group Cervidae dynamics and the male leader that is usually the one most successful in fights. However, some of the harem winners failed to develop antlers and these "hummels" put sexual selection based on antlers and fighting into question.
- The article also outlines some of the known history of the divergence between Bovids and Cervidae, as well as that horns originated in reptilian animals and passed on to Bovidae. Antlers came later.

5. Insight into gene evolution within Cervidae and Bovidae through genetic variation in MHC-DQA in the black muntjac (Muntiacus crinifrons)

- Wu, H. L., et al. "Insight into Gene Evolution within Cervidae and Bovidae through Genetic Variation in MHC-DQA in the Black Muntjac (Muntiacus Crinifrons)." *Genetics And Molecular Research*: GMR, vol. 11, no. 3, Aug. 2012, pp. 2888–2898. *EBSCOhost*, search.ebscohost.com/login.aspx?direct=true&db=cmedm&AN=22653641&site=ehost-live.
- This study explores the small level of variation in black muntjac deer possibly due to bottlenecks, solitary behavior, and strong natural selection. Studies the DQA alleles that remain in both Cervidae and Bovidae since right before their divergence 25.5 to 27.8 million years ago, suggesting that these alleles have lasted in the DNA for that extended period of time. Each family showing its own set of mutations throughout.

6. Evolution and phylogeny of old world deer

- Pitra, Christian, et al. "Evolution and Phylogeny of Old World Deer." *Molecular Phylogenetics and Evolution*, vol. 33, no. 3, 2004, pp. 880–895., doi:10.1016/j.ympev.2004.07.013.
- This is a study that focuses on Old World Deer (OW Deer) because of the lack of research of their traits and evolution. OW deer, or Cervinae, are a subfamily within Cervidae. Cyt b was chosen as a molecular marker to analyze phylogenic relationships between OW deer and other Cervid subfamilies, as it has large sequence variation. The study strongly advocates for homoplasy among antlered Cervidae and a connection to environmental aspects that affect the shape of antlers.

7. Evolution of the Vertebrates: A History of the Backboned Animals Through Time (2nd ed.)

- Colbert, Edwin H. *Evolution of the Vertebrates: A History of the Backboned Animals Through Time*. 2nd ed., John Wiley & Sons, Inc., 1955.
- This book's chapter outlines some of the horned ancestors of Bovids and antlered ancestors of Cervids. Protoceras has six separate horns. It discusses the growth in size of antlered deer along with the size of their antlers. This book suggests that horns are used frequently for aggression due to their strength. It questions why there are so many variations in headgear within the same family among species that generally live in the same environment and makes an attempt to answer the question by suggesting populations that split and evolved separately. The chapter ends with: "No attempt will be made to describe the bovoids."

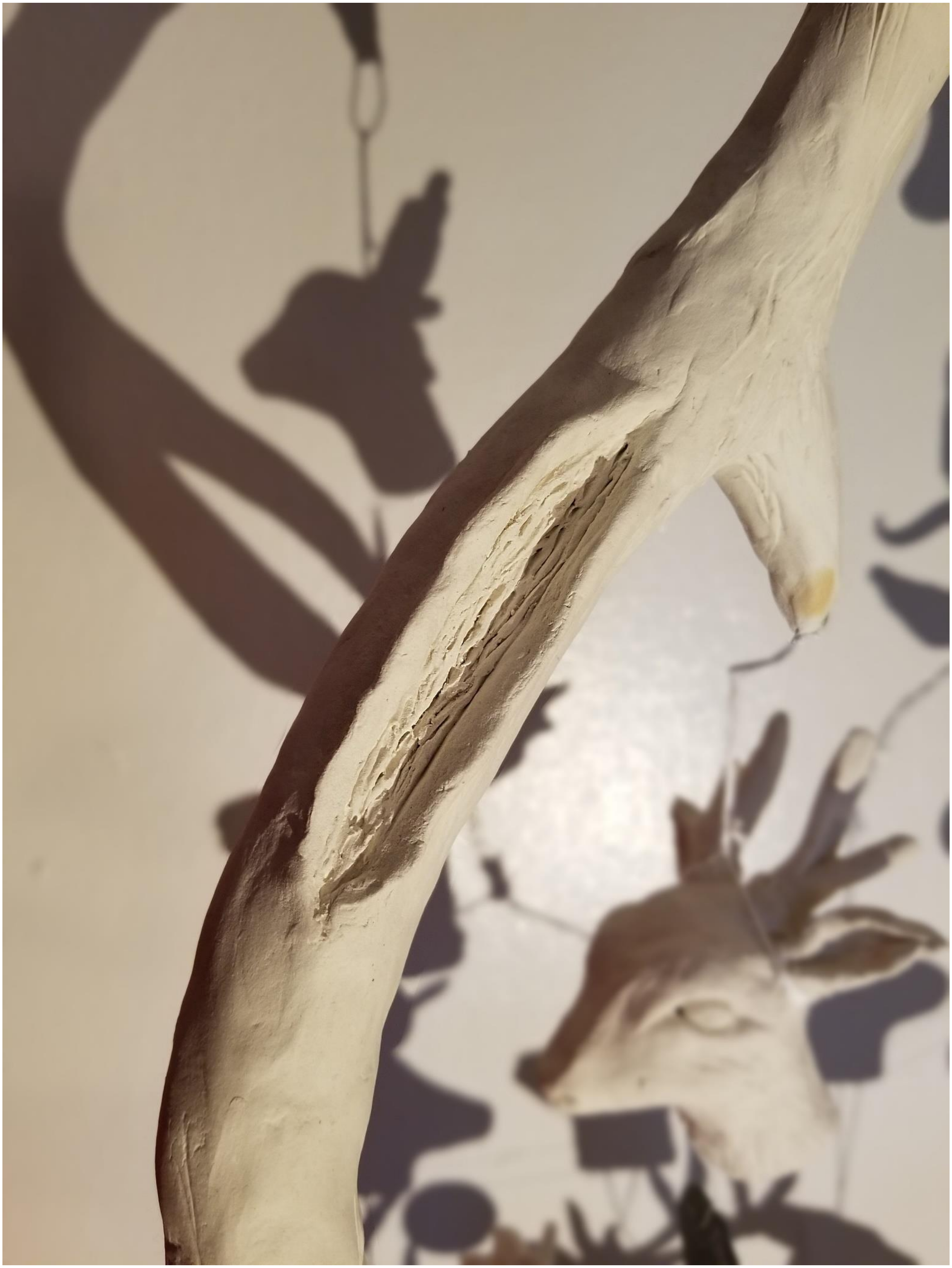
8. Major-Histocompatibility-Complex-Associated Variation In Secondarysexual Traits Of White-Tailed Deer (Odocoileus Virginianus): Evidencefor Good-Genes Advertisement

    - Ditchkoff, S S, et al. "Major-Histocompatibility-Complex-Associated Variation in Secondary Sexual Traits of White-Tailed Deer (Odocoileus Virginianus): Evidence for Good-Genes Advertisement." *Evolution; International Journal of Organic Evolution, U.S. National Library of Medicine*, Mar. 2001, www.ncbi.nlm.nih.gov/pubmed/11327168.
    - This study gives insight to sexual selection based on antler size and what the size tells about the male's overall genetic fitness. The study suggests this could be the reason that females select males based on the size of their antlers – the antlers being a proxy trait.


SMALL
animal
RUN + HIDE
FOREST
PREDATORS


SMALL
RUN + HIDE
OPEN
LARGE ANIMAL
ATTACK PREDATORS
MATING DISPLAY
SAVANNA

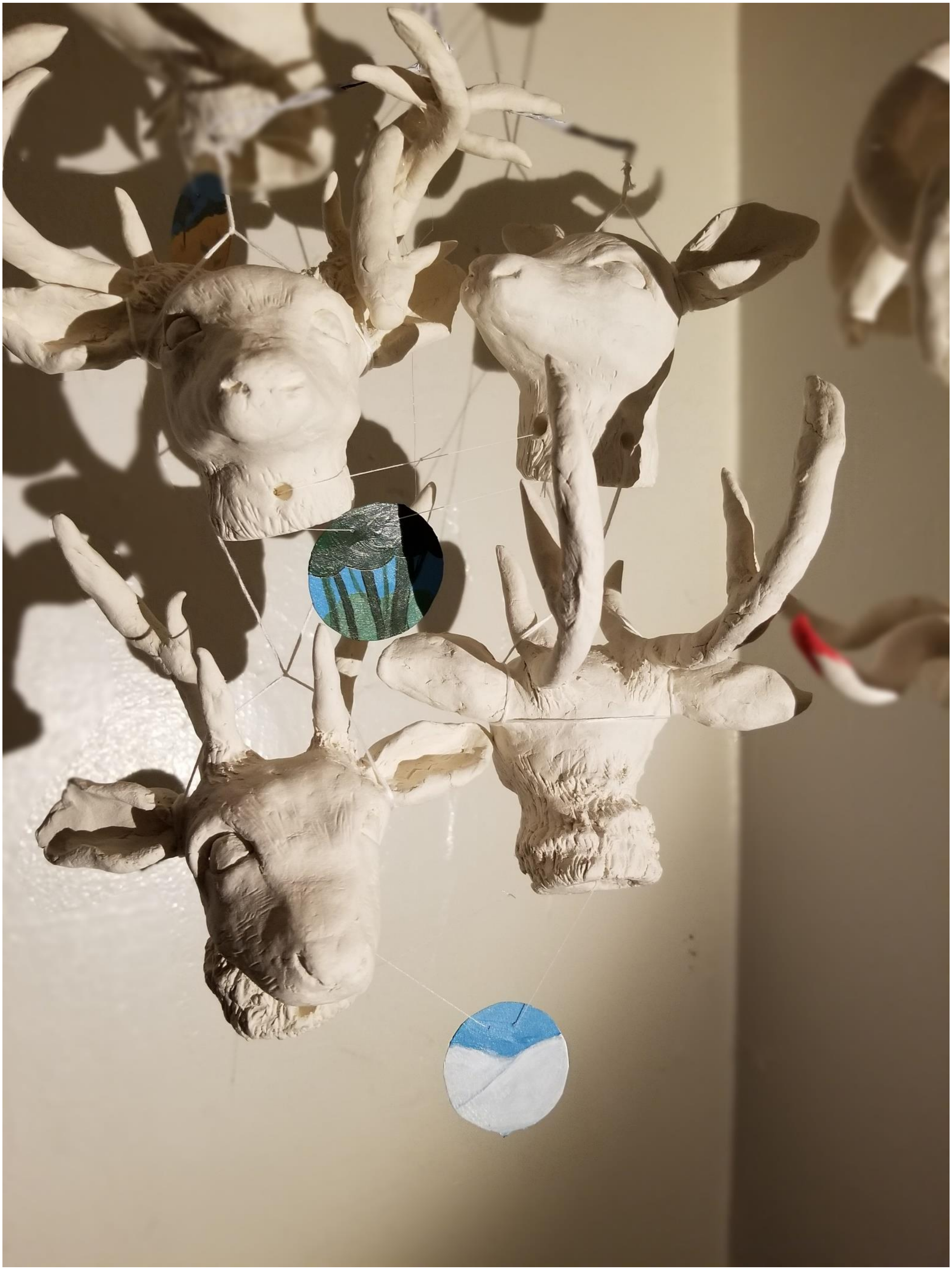

OPEN
areas
RUN FROM LARGE
PREDATORS
FIGHT SMALL
PREDATORS
SAVANNA



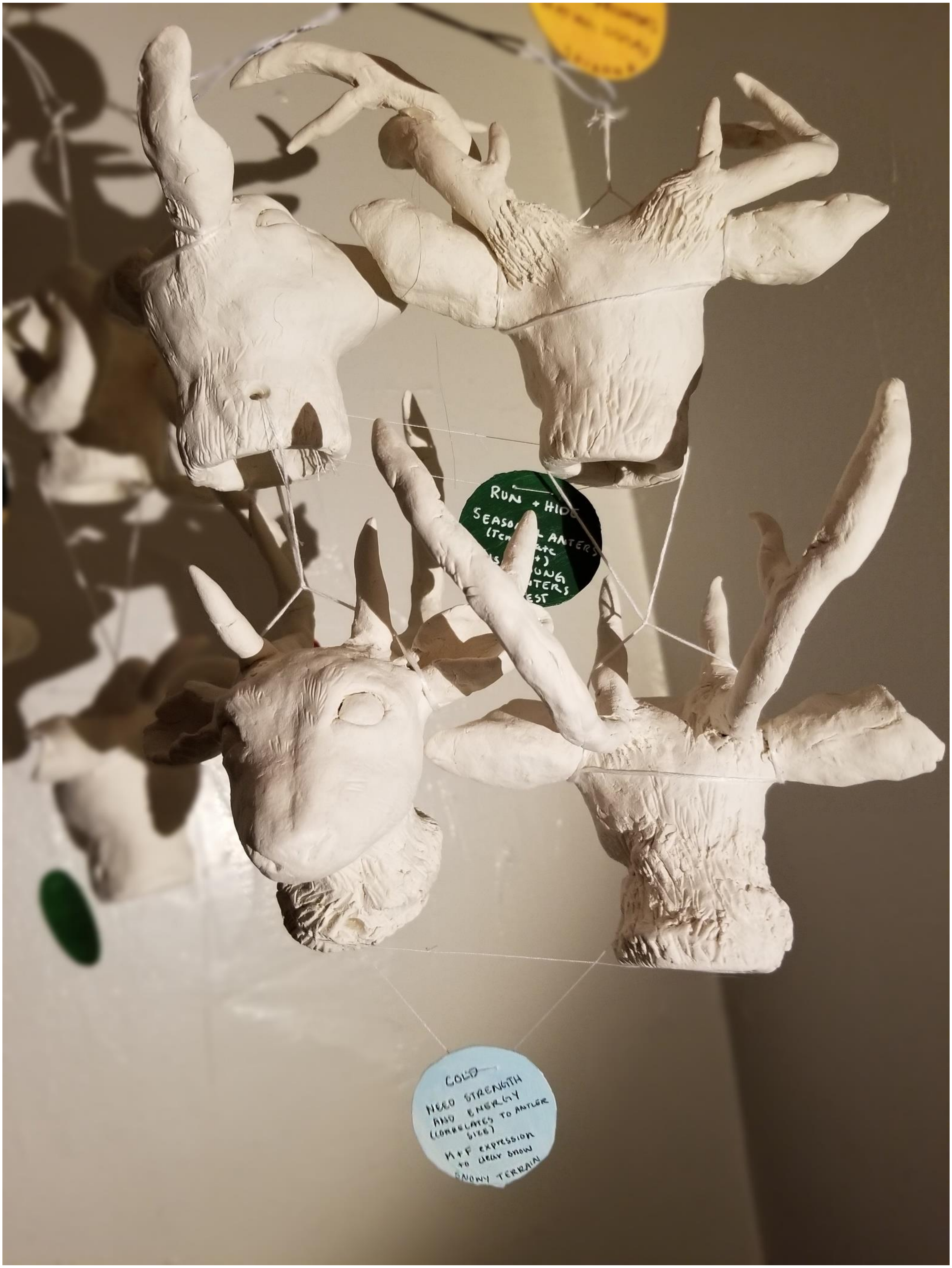
Inside of antler

Dicrocerus

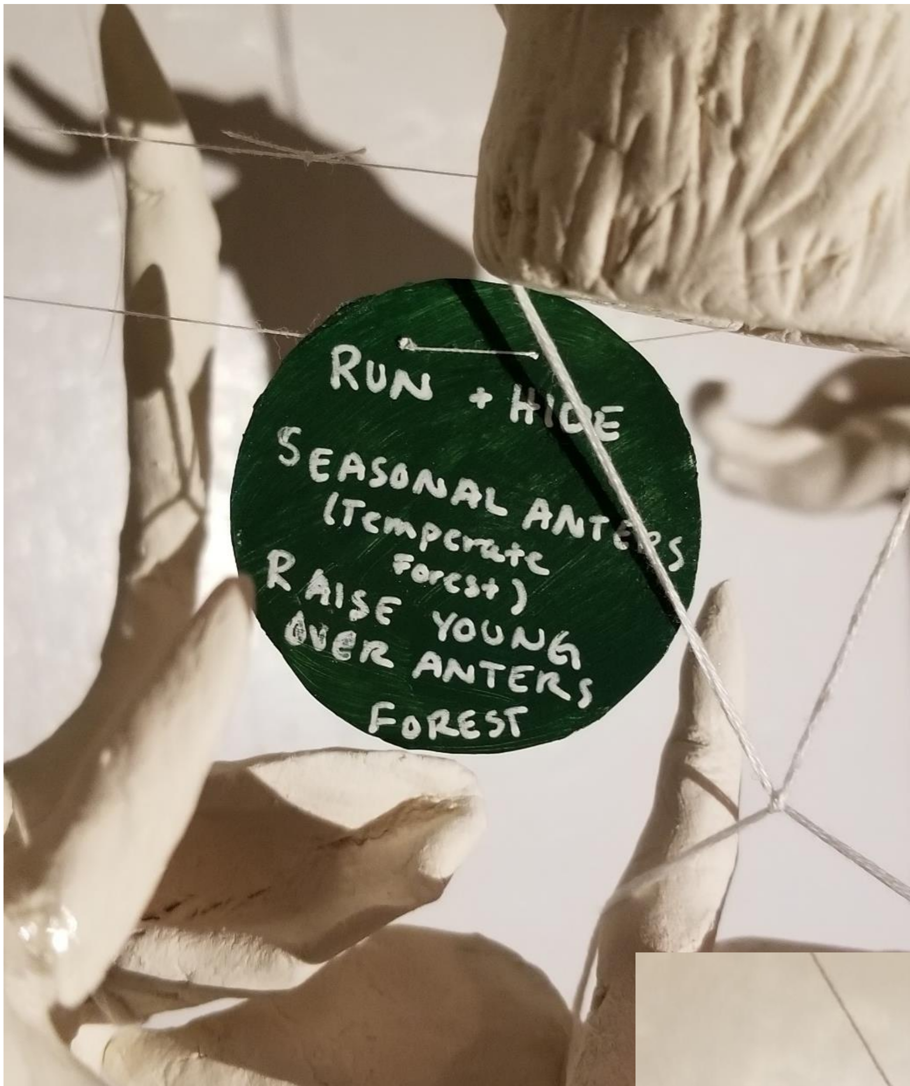
Libralces gallicus



White-tailed deer – top row
Reindeer – bottom row

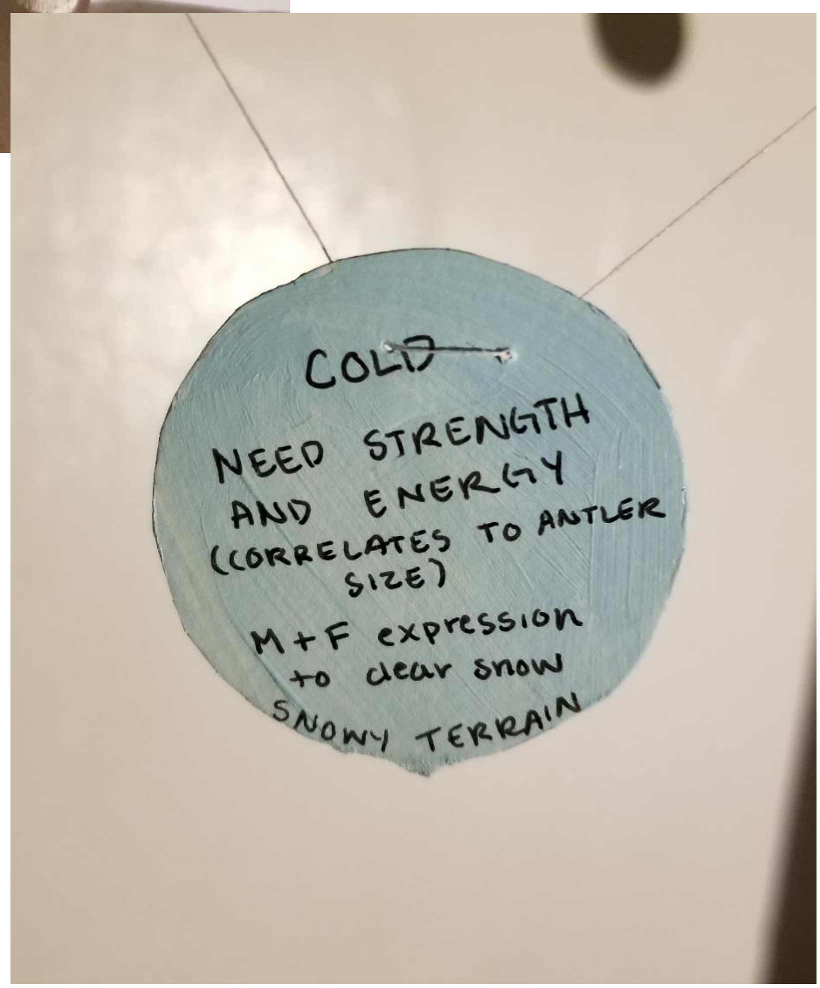


White-tailed deer – top row
Reindeer – bottom row



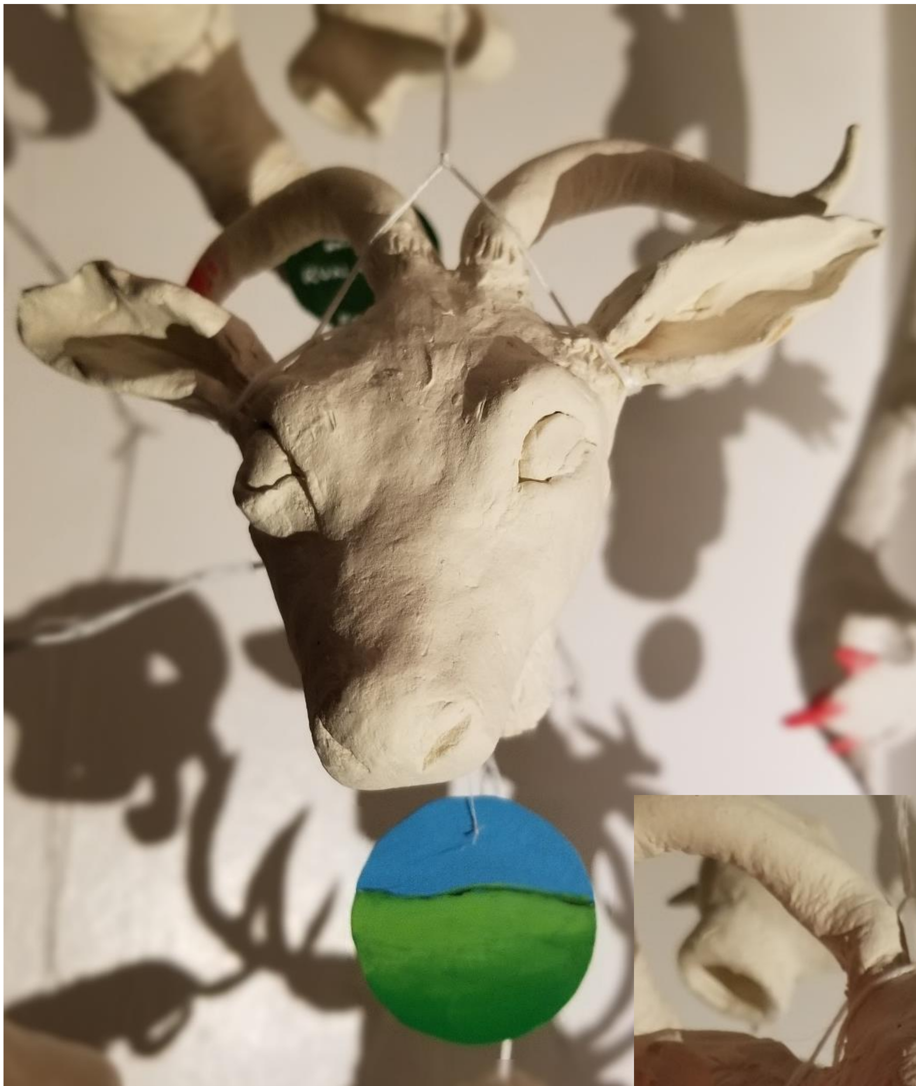
→ Description of white-tailed deer environment

Description of reindeer environment ←

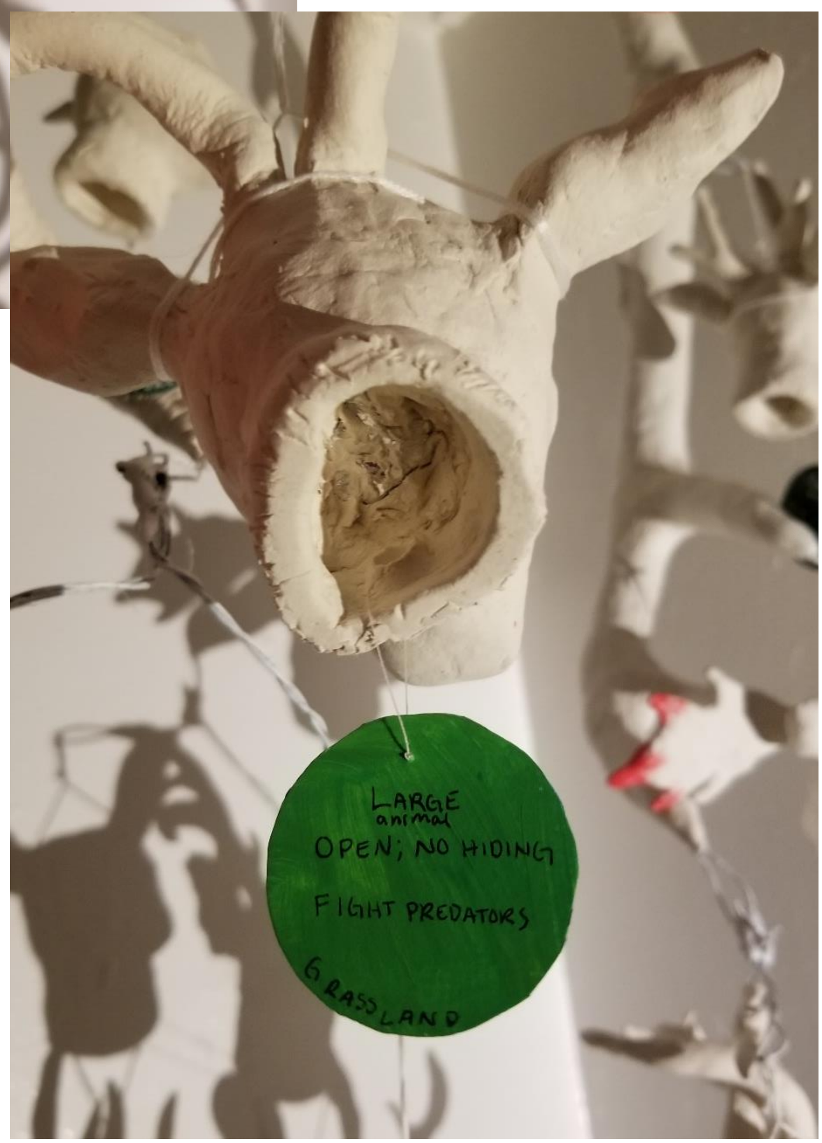


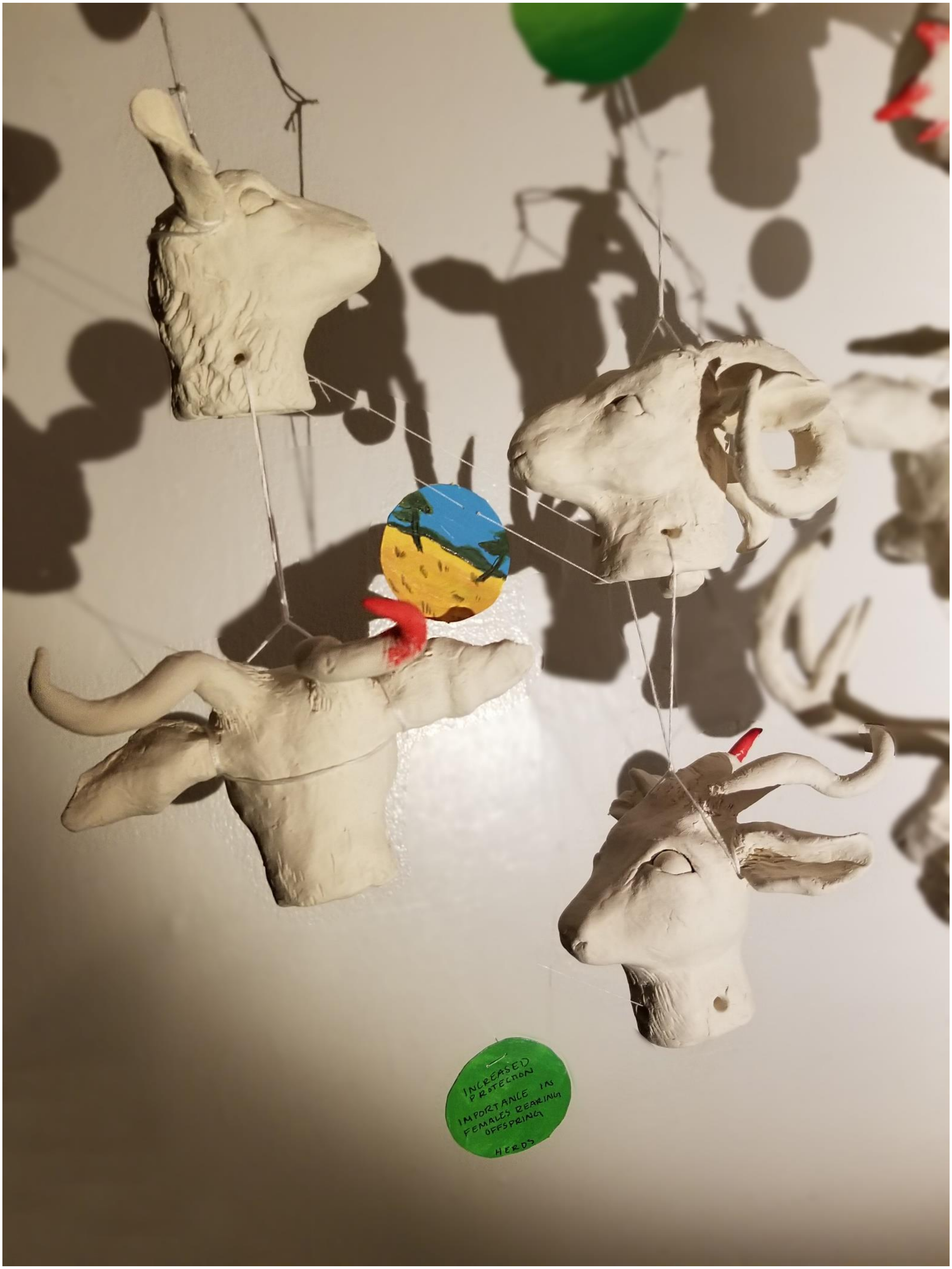
Inside of horn

Eotragus



Megalotragus





Black Welsh mountain sheep – top row
Dama gazelle – bottom row

Black Welsh mountain sheep

Dama gazelle